FOOD WEBS

FROM NATURAL TO PRODUCTION FORESTS:

COMPOSITION, PHYLOGENY AND FUNCTIONING

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‘Bound together by a web of complex relations’

C. Darwin

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Abstract

Habitat loss and fragmentation have been identified as the main drivers of biodiversity loss. These drivers increase the proportion of habitat edges and change the configuration of landscapes. Habitat edges are known to affect ecological patterns and processes, however, is still unknown how these boundaries affect the assemblage of interactions among species within a community, and particularly its structure. Food webs depict not only the composition of the community, but also the feeding links, which represent a measure of energy flow. Therefore, they can inform about the relationships among community diversity, stability, and ecosystem functions.

This thesis explores the effects of habitat edges across native vs. managed forests on the food web of a tri-trophic system comprising plants, herbivores (Lepidoptera larvae) and predators (parasitoids). Particularly, it addresses three main objectives: 1) how food webs at habitat edges are assembled from the species and interactions present in the adjoining habitats; 2) how phylogenetic diversity and the coevolutionary signal among interacting species change across a habitat edge gradient; and 3) whether the mechanisms driving community-wide consumption rates and the ecosystem service of pest control are related to structural characteristics of the food webs.

The key findings of this thesis are that, despite the composition of species and interactions of native and managed habitats merging at their interface, food-web structure did not arise as a simple combination of its adjacent habitat webs, potentially due to differential responses of organisms to habitat edges. Moreover, beyond taxonomic composition, the phylogenetic diversity and signal of coevolution among

interacting species also change between habitat types, even though this did not translate to changes in consumption rates. Consumption rates and their stability increased with complementarity and redundancy in resource-use among predators.

This reflects how environmental changes such as habitat fragmentation can have an effect beyond composition *per se*, affecting the assemblage of species interactions and even potentially interfering with natural evolutionary processes. Therefore, using interaction-network approaches for determining the impacts of changes may shed light on the underlying mechanisms driving such changes, and help to develop landscape management plans that reduce negative effects on species assemblages.

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Chapter I

Introduction

1.1 Global environmental change and modern ecosystems

Modern ecosystems are mostly the result of centuries of human population and geographic expansion. Humans have modified the environment in many different ways, altering its physical and biogeochemical components to increase food production, extract minerals, construct urban areas, and build industries, among others. As a result, landscapes have been highly transformed and degraded, with not very encouraging perspectives for recovery in the coming years (Tilman *et al.* 2001; IPCC 2002; Foley *et al.* 2005; Millenium Ecosystem Assessment 2005; Barnosky *et al.* 2011).

The extent to which humans have changed the use of land, altered nutrient cycles and modified climatic conditions (Sala *et al.* 2000), has precipitated a steep increase of species extinction rates (Pimm *et al.* 1995), i.e. biodiversity decline (Chapin *et al.* 2000; Tilman & Lehman 2001). Biodiversity decay not only impacts the aesthetic and cultural values of ecosystems to humans (Chapin *et al.* 2000), but it also has detrimental effects on beneficial ecosystem services such as biological control, pollination and decomposition (Naeem *et al.* 1994; Chapin *et al.* 2000; Loreau *et al.* 2001; Dobson *et al.* 2006), which underpin human well-being (Díaz *et al.* 2006).

Despite all the known effects of environmental change on biodiversity, less attention has been paid to the interdependencies among interacting species (Janzen 1974; McCann 2007; Tylianakis *et al.* 2008a), which can drive indirect effects between species. This is why it has been suggested that, to completely understand the effects of environmental changes, it

is critical to monitor the interactions among species (McCann 2007; Tylianakis *et al.* 2008a), which may in the future allow us to predict the direction of ecosystem outcomes.

1.1.1 Shaping ecosystems: biodiversity and species interactions

In ecosystems, organisms do not behave like independent entities, but rather they interact with each other in many diverse ways. Different types of relations/links among organisms exist, such as predation, competition and mutualisms, which generate a complex web of interactions (Pimm 1982; Paine 1988; Thompson 2006; Bascompte 2009; Kéfi *et al.* 2012) that gives structure to biodiversity. The study of interaction networks therefore generates a more complete understanding of the ecosystem, since they not only include the species composition but also the links among those species, which represent a measure of energy flow within the web (Thompson *et al.* 2012). Also, because interaction networks are sensitive to the presence, abundance, phenology, behavior and physiology of the multiple interacting species (Voigt *et al.* 2003; Memmott *et al.* 2007; Suttle *et al.* 2007), they are likely to show changes even before the loss of species occurs (Tylianakis *et al.* 2008a). Therefore, interaction networks represent a promising tool for understanding, managing and conserving ecosystems in the face of global environmental change (Bascompte 2009; Brose 2010; Tylianakis *et al.* 2010).

Of the different types of interaction networks, potentially the most research attention has been paid to 'food webs', which describe the feeding interactions between organisms. Each trophic link within a food web not only represents the ingestion of individuals by other individuals, but also the associated flux of biomass, energy, nutrients and trace elements that move across trophic levels (Woodward *et al.* 2005; Rooney *et al.* 2006; Thompson *et al.* 2012). This makes food webs suitable not only for describing communities, but also for

analyzing their dynamics, as well as their relationships and effects on ecosystem functioning and stability (May 1973; Pimm 1982; Montoya *et al.* 2003; Brose 2008; Macfadyen *et al.* 2009; Thébault & Fontaine 2010; Poisot *et al.* 2013).

1.2 Interaction networks, the missing link to understanding fragmentation

In global environment terms, habitat loss and fragmentation are the most important direct drivers of community change and biodiversity loss (Sala *et al.* 2000; Millenium Ecosystem Assessment 2005), with fragmentation defined as the process by which a large habitat is transformed into smaller patches, isolated from each other by a matrix of a different habitat type (Wilcove *et al.* 1986). Recent research has shown how these drivers can have effects beyond biodiversity *per se*, by altering the community assemblage of trophic interactions, i.e. food webs. For example, it has been observed that i) habitat loss leads to food-web contraction, with only a core of highly connected species left in the smaller fragments (Valladares *et al.* 2012); ii) modification of natural habitats alters food-web structure, even when no changes on biodiversity are observed (Tylianakis *et al.* 2007); iii) agricultural intensification can increase the complexity of food webs (Gagic *et al.* 2012) and iv) restored habitats can harbour higher diversity of interactions than adjacent managed habitats (Albrecht *et al.* 2007). However, fragmentation not only changes the spatial configuration of habitats, but also increases the proportion of edge relative to interior habitats (Fahrig 2003), which are usually ecologically distinct (Ries *et al.* 2004).

Many of the ecological alterations faced by fragmented habitats (e.g. disruption of species interactions, species loss, and species invasion) can be assigned to 'edge effects'

(Fahrig 2003), which can influence even small organisms such as invertebrates (Bellinger *et al.* 1989; Didham 1997; Chacoff & Aizen 2006; Ewers & Didham 2008). Habitat edges usually have different abiotic conditions (Murcia 1995) and high rates of species movement (Rand & Louda 2006; Macfadyen & Muller 2013) compared with habitat interiors, which influence the establishment of species. Experimental and theoretical studies have demonstrated that habitat edges can strongly influence species diversity (Woodroffe & Ginsberg 1998), species coexistence (Sears *et al.* 2004) and community stability (Huxel & McCann 1998; Holt 2002). Even more, edges can affect species interactions through several mechanisms, such as altering movement patterns (Macfadyen & Muller 2013), inducing mortality (Valladares *et al.* 2006), functioning as cross-boundary subsidies (Rand *et al.* 2006), or as a unique habitat type (Fagan *et al.* 1999), and thus have an impact on community dynamics.

It has also been suggested that edge habitats might be 'hyper dynamic', exhibiting increased variability and less stable community structure than habitat interiors (Laurance 2002), due to differential responses of species (in terms of their abundance, distribution and interactions) to this type of habitat. This, along with the differential movement of organisms across habitats (Rand *et al.* 2006; Macfadyen & Muller 2013), suggests that large-scale edge responses may be driven more by variation in biotic interactions than by environmental conditions (Ewers & Didham 2008). Therefore, the influence of edges on food webs, and particularly the way in which interactions from adjacent habitats assemble at edges, would be expected to be fundamental to a broader understanding of ecological dynamics in fragmented systems.

1.3 Evolutionary history and species interactions

The incorporation of evolutionary information into ecological studies has been increasing in the last decade (Webb *et al.* 2002; Cavender-Bares *et al.* 2009; Mouquet *et al.* 2012), with a shared evolutionary history of related species making them similar due to inheritance of traits from a common ancestor (Felsenstein 1985; Harvey & Pagel 1991). Thus, more closely-related species are ecologically more similar (Burns & Strauss 2010), and relatedness can therefore provide additional information regarding the diversity of a community, including the diversity of traits (Helmus *et al.* 2007), and hence its susceptibility to anthropogenic environmental changes (Díaz & Cabido 1997).

Recent research has demonstrated how global-change drivers can affect the phylogenetic composition of communities. For example, climate change (temperature increase) leads to phylogenetically selective patterns of changes in the abundance of species, with closely-related species decreasing in abundance (Willis *et al.* 2008). Also, habitat disturbance has been shown to generate phylogenetic homogenization of communities (Dinnage 2009; Helmus *et al.* 2010), with the same pattern observed in the face of species loss (Winter *et al.* 2009). The prevalence of only certain clades in communities could reduce the capacity of communities to respond to environmental changes (Knapp *et al.* 2008), via a decrease in trait variability. This highlights the importance of taking into account the phylogenetic identity of species, as well as their taxonomic identity, when assessing the effects of environmental change.

Phylogenetic relationships among species have been shown to predict the diversity of the organisms with which they interact (Dinnage *et al.* 2012), and even the interaction patterns in networks and the potential for coextinction cascades of related species (Rezende *et al.* 2007). Overall, phylogenetic diversity provides a link between evolution, species traits

relevant for functioning and species interactions. Hence, the incorporation of species relatedness into the study of species interactions can allow forecasting of the dissemination across entire ecosystems of non-desirable effects of human-induced changes (Rezende *et al.* 2007). Despite this, the effects of one of the most pervasive features of fragmentation, habitat edges, on phylogenetic diversity across different trophic levels have not yet been assessed.

1.4 Shaping ecosystem functions: biodiversity and species interactions

Changes in the ecosystem functions that make human life possible are among the major threats of species loss (Chapin *et al.* 2000; Díaz *et al.* 2006). Consequently, a lot of research has focused on the relationship between biodiversity and ecosystem functioning (BEF) (Tilman *et al.* 1996; Cardinale *et al.* 2000; Loreau *et al.* 2001; Naeem & Wright 2003; Hooper *et al.* 2005), as well as between diversity and functional stability (Naeem & Li 1997; Yachi & Loreau 1999; McCann 2000; Tylianakis *et al.* 2006; Ives & Carpenter 2007).

Consumer-resource or predator-prey interactions have been widely studied in the context of BEF (Sih *et al.* 1998; Duffy 2002; Casula *et al.* 2006; Finke & Snyder 2008; Striebel *et al.* 2012; Schneider & Brose 2013), given the high impact that these interactions have on ecosystem functions, such as biological control and pollination, and their stability (Cardinale *et al.* 2003; Klein *et al.* 2003; Cardinale *et al.* 2004; Snyder *et al.* 2006; Macfadyen *et al.* 2011). Many of these studies have focused on the responses of few species (Ives *et al.* 2005; Cardinale *et al.* 2006; Duffy *et al.* 2007) due to logistical limitations or because they were interested in the response of particular species. However, studying ecosystem functions at small scales can have the drawback of potentially overlooking emergent community effects (Letourneau *et al.* 2009). Moreover, it has been suggested that

the pattern of interactions among species might play an essential role in determining ecosystem functions (McCann 2007), and hence the link between biodiversity and ecosystem functioning could have more to do with how species interact than how many species form the community (Montoya *et al.* 2003).

Therefore, interaction networks have been identified as beneficial tools for assessing changes in ecosystem functions at the community level because, by incorporating species interaction patterns, the flow of energy within the community and the patterns of resource use are taken into account (Thompson *et al.* 2012). Even more, food webs may provide the necessary information to unravel the mechanisms driving ecosystem functions (Poisot *et al.* 2013) and their stability, which is essential for ameliorating the effects of global environmental change.

1.5 Thesis outline and objectives

This thesis is structured in five chapters, opening with a general introduction (**Chapter I**), followed by three data chapters, each written as a manuscript for submission to peer-reviewed journals. The final chapter (**Chapter V**) summarizes the findings of all the chapters, and highlights areas for future research. The overall aim of this thesis was to use a food-web approach to determine how habitat edges affect community composition, interactions within the assemblage, and ecosystem functioning. I particularly focused on food webs since they provide information about composition and structure of communities, and hence address community patterns as well as the mechanisms behind them. Moreover, I chose to study food webs across a habitat edge gradient because edges are ubiquitous in contemporary fragmented landscapes, and they also exert a strong influence on the degree of connection among different habitats in the landscape (Stamps *et al.* 1987).

To accomplish this aim, I studied a system of interacting plant-herbivore-parasitoid communities (Fig. 1.1), organisms which comprise ca. 60 % of the known species on earth (La Salle & Gauld 1991; Hawkins 1994). The outcome of these interactions ultimately determines rates of parasitism and herbivory, two key ecological functions in natural and human-dominated ecosystems. I sampled these organisms across a habitat edge gradient between native and managed forest types (Fig. 1.2). For this, I selected eight different sites in which *Pinus radiata* production forest grows adjacent to native southern beech forest (*Nothofagus spp.*), located in the Nelson and Marlborough regions in New Zealand.

The first specific aim of this thesis was to determine whether the community composition of different trophic levels changes across a habitat edge gradient, and whether habitat edges affect the way in which species interactions assemble to form food webs. Specifically, I wanted to determine whether food webs at habitat edges are formed by a random combination of interactions from the adjacent habitats. Therefore, **Chapter II** examines the community composition across a habitat edge gradient, as well as how the food-web composition and structure of habitat edges differs from what would be expected by simply merging the species and interactions from the two adjacent habitats.

Determining how edge habitats affect the network of interactions among species could uncover species that might be favoured in such habitats. However, by only analysing species according to their individual identities, we might miss important effects of habitat edges on certain clades, due to the phylogenetic non-independence of species response traits. Thus, **Chapter III** explores changes in the phylogenetic diversity of different trophic levels across a habitat edge gradient. Moreover, by combining phylogenetic information with species interaction patterns, this chapter addresses how the strength of any coevolutionary signal between trophic levels changes across habitats.

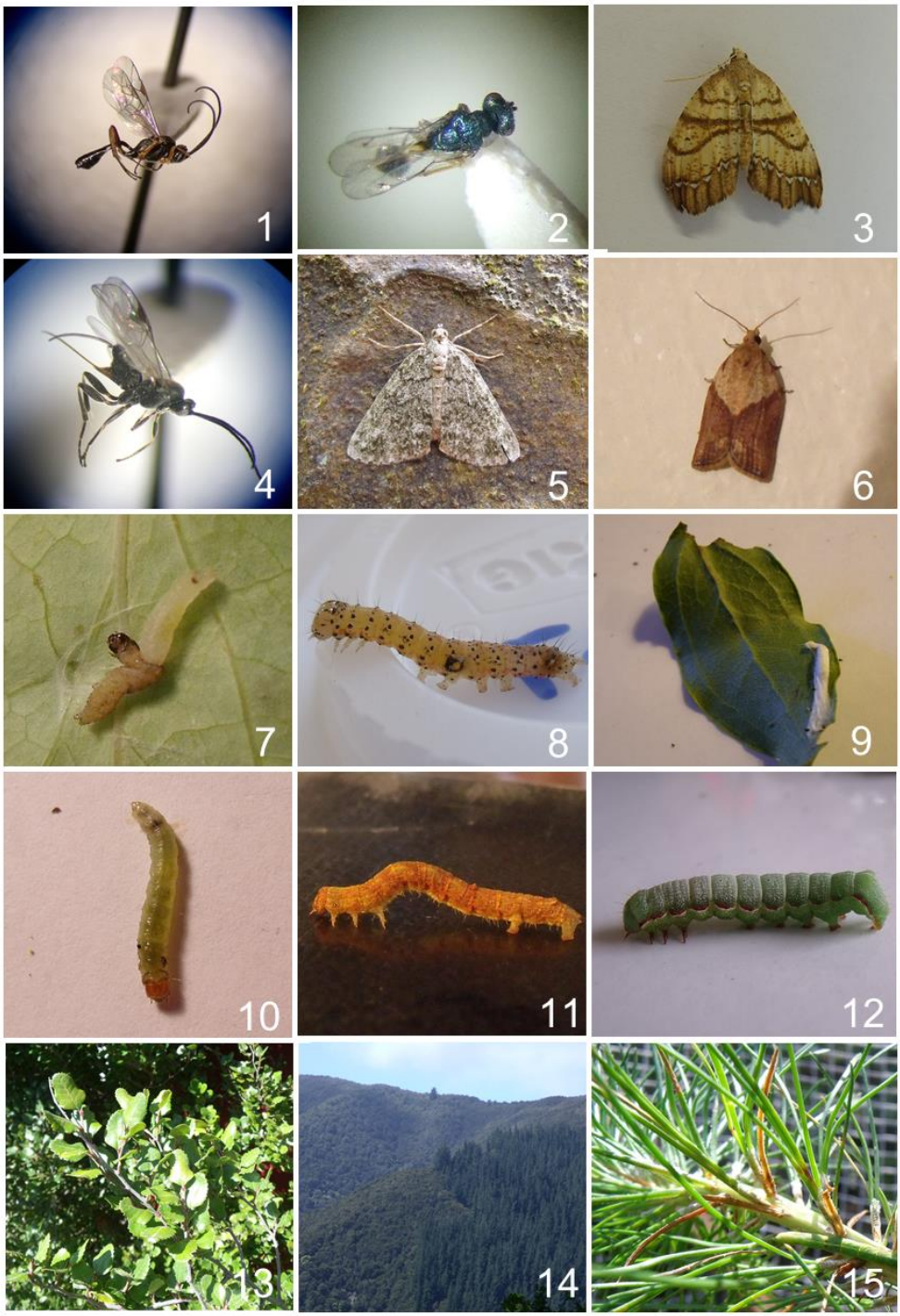

Figure 1.1: Plant-herbivore-parasitoid communities. **Adult parasitoids:** 1) *Diadegma sp.* (Ichneumonidae); 2) *Zealachertus sp.* (Eulophidae) and 4) *Dolichogenidea sp.* (Braconidae). **Adult Lepidoptera:** 3) *Chalastra pellurgata* (Geometridae); 5) *Pseudocoremia suavis* (Geometridae); 6) *Epiphyas postvittana* (Tortricidae). **Parasitoid larvae:** 7) emerging from Tortricidae larvae; 9) Parasitoid pupae. **Lepidoptera larvae:** 8) *Feredayia graminosa* (Noctuidae) with a hole on its side from a parasitoid emergence; 10) *Ctenopseustis sp.* (Tortricidae); 11) *Declana floccosa* (Geometridae); 12) *Meterana dotata* (Noctuidae). **Plants:** 13) *Nothofagus fusca* (Nothofagaceae) main tree species in the native forest; 14) Edge between native and pine forests; 15) *Pinus radiata* (Pinaceae) main tree species in the plantation forest. Photos by G. Peralta.

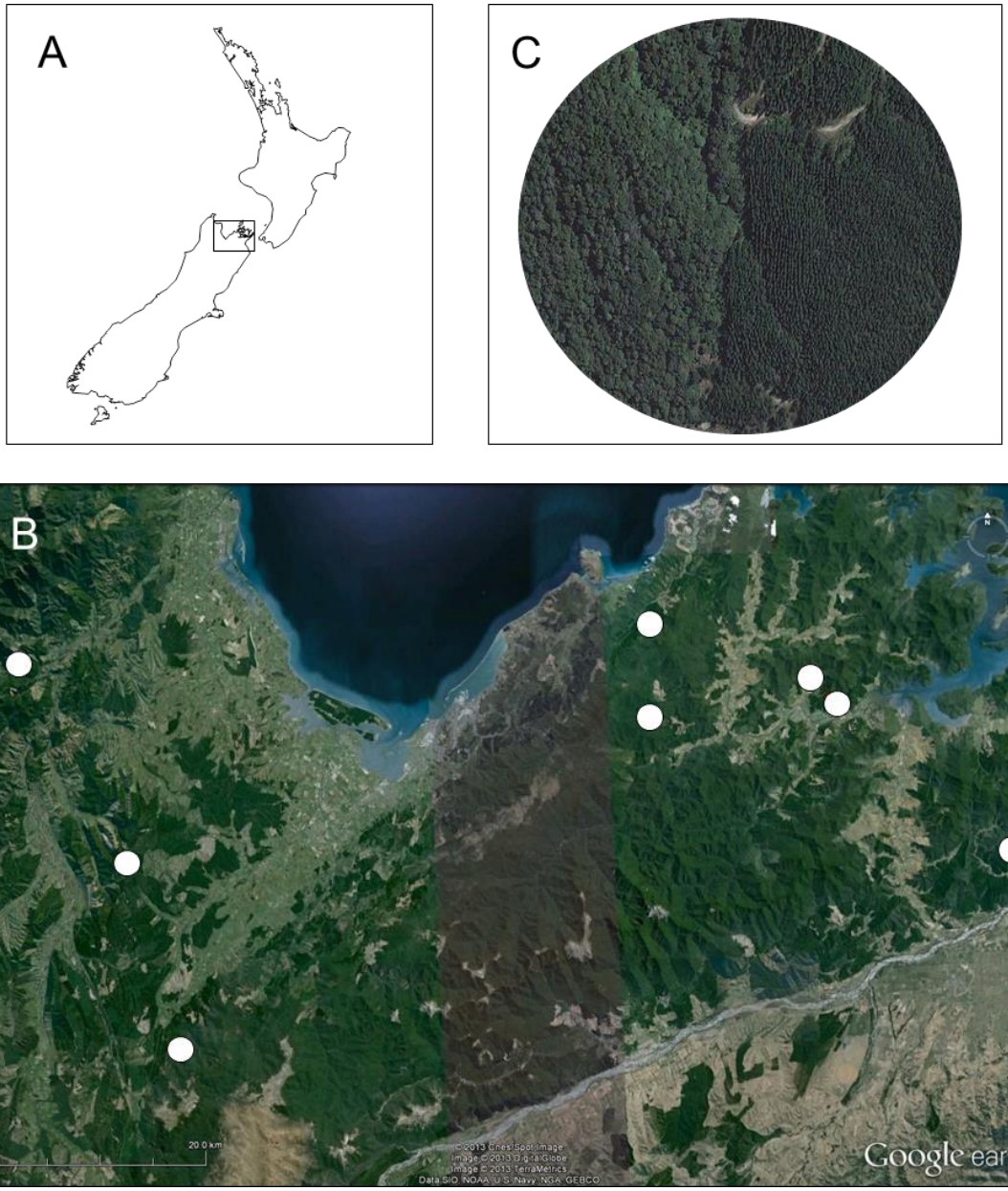

Figure 1.2: Study region and sampling sites. A) Map of New Zealand with study region (Nelson/Marlborough areas) marked by square. B) Enlargement of the study region showing the eight sites selected for the study. C) One of the sampling sites showing the edge gradient between native southern beech forest and pine plantation forest.

Changes in land use and the formation of habitat edges can also impact ecosystem functions and their stability, often through changes in biodiversity. However, even though biodiversity might be related to changes in ecosystem functioning, this pattern in itself does not explain the mechanisms driving these changes. Small-scale experimental studies have suggested resource-use complementarity (i.e. niche partitioning) as a potential mechanism

driving biodiversity effects on ecosystem functions (Finke & Snyder 2008), although large-scale empirical studies have not yet determined whether this mechanism can be extrapolated to entire communities. Therefore, by using the food webs sampled in the previous chapters, **Chapter VI** examines whether complementarity in resource use affects the ecosystem function of (host) resource consumption by parasitoids. Because not only the magnitude of ecosystem functions, but also their stability in time and space are important, I tested whether redundancy in resource use would favour stability of parasitoid-host interactions, as predicted by the insurance hypothesis (Yachi & Loreau 1999). Finally **Chapter V** synthesises all the findings and highlights potential areas of future research.

Chapter II

Merging of species at habitat boundaries creates novel interaction-network structure

2.1 Abstract

Habitat conversion for human use is dramatically increasing the extent of edges between native and managed ecosystems. Edge effects not only alter relative abundances of species, but also their feeding interactions. Despite the important role that food-web structure plays in the ability of ecosystems to resist perturbations and persist over time, it is not known how the very different food-web structures observed in natural versus managed ecosystems merge across ecosystem boundaries.

Here I examined whether the structure and composition of edge food webs (quantitative networks of feeding interactions) can be predicted from those of the adjacent communities, by testing three alternative hypotheses: 1) edges mark a clear distinction in composition between adjacent communities, such that webs at edges contain two separate compartments (*'non-stick' webs*), 2) both the species composition and interaction structure of adjacent communities merge at edges, such that the edge web contains a random sample of the interactions present in the two adjacent habitats (*'blended' webs*), and 3) mixing of species at edges results in novel food-web structures, which are not predictable by merging the adjacent habitat webs (*'hyper' webs*). At the edges of native forest remnants adjacent to

exotic pine plantations in New Zealand, I characterized the composition and structure of herbivore-parasitoids food webs, which were used to test these hypotheses.

I found that habitat edges did not mark a clear division in community composition between adjacent areas, but rather that spillover of species might play an important role in the formation of edge webs. Moreover, although edge food webs displayed a degree of blending in community composition, their structure did not simply arise through the combination of their adjacent habitat webs, i.e. edge food webs were not a random sub-sample of interactions from the neighbouring areas. Instead, edge webs combined in a more complex manner, leading to a novel network of feeding interactions. This observation provides support for the '*hyper*' web hypothesis, and was probably due to differential responses of species to habitat edges.

Advances in the understanding of food-web structure and assembly at habitat edges have important applied implications for biological control in managed habitats and for quantifying the direct and indirect effects on native systems of species in productive habitats.

2.2 Introduction

Habitat loss and fragmentation are among the main causes of biodiversity loss and species extinction globally (Sala *et al.* 2000; Fahrig 2003; Krauss *et al.* 2010). Fragmentation dramatically changes the composition and spatial configuration of habitats in the landscape, with the creation of artificial edges being one of the most pervasive outcomes of human land-use change. Edges are a focal point for ecological change in ecosystems, and research on anthropogenic edges has developed out of a long history of interest in natural ecotones and ecosystem boundaries (Hansen & Castri 1992; Knight *et al.* 2005; Martin *et al.* 2007).

Habitat edges can influence patterns of species abundance, distribution and diversity (Fowler *et al.* 1993; Dyer & Landis 1997; Ewers & Didham 2008), and alter dispersal processes (Duelli *et al.* 1990; Blitzer *et al.* 2012) and species interactions (Fagan *et al.* 1999; Ries *et al.* 2004; Ewers *et al.* 2013). For example, species diversity often increases at edges relative to interior habitats (Ries *et al.* 2004; Ewers & Didham 2008) due to increases in populations of generalists that utilise resources in multiple habitats (Fagan *et al.* 1999) and move across habitat boundaries (Didham *et al.* 1996). Edges can also change species abundances, which appear to depend on species-specific susceptibility to habitat modification (Ewers & Didham 2008). Some species have been observed to decline in numbers near edges (Fowler *et al.* 1993; Didham *et al.* 1998; Ewers & Didham 2008), while others have been shown to increase in abundance (Ewers & Didham 2008; Leidner *et al.* 2010). The high variability of edge effects on species within communities has the potential to increase the frequency and/or amplitude of ecological dynamics (Huxel & McCann 1998; Fagan *et al.* 1999; Holt 2002) and variability in ecosystem functions (Thies & Tscharntke 1999; Valladares *et al.* 2006). This has been termed 'hyperdynamism' in edge processes (Laurance 2002), and has been observed to affect trophic interactions such as parasitism on leafminers in forest remnants (Valladares *et al.* 2006).

Changes in community structure and consumer dynamics have the potential to alter the structure of food webs (Huxel & McCann 1998; Holt 2002). Given that the structure of food webs plays an important role in maintaining ecosystem function (Montoya *et al.* 2003; Thompson *et al.* 2012) and community stability (e.g. Montoya *et al.* 2006; Thébault & Fontaine 2010), detecting changes in food-web structure is central to our understanding of community responses to, and ecological dynamics within, fragmented systems. Framing fragmentation effects in a food-web context also increases the potential to detect subtle responses to environmental change, because of the sensitivity of food-web structure to the

presence, identity, phenology and behaviour of multiple species. Thus, food webs are likely to show community changes before a loss of diversity becomes apparent (Sabatino *et al.* 2010).

Even though food-web structure can differ across habitats (Tylianakis *et al.* 2007), surprisingly little is known about how this structure is generated or altered at the edges between habitats and ecosystems, beyond widespread evidence for changes in pair-wise species interactions (Fagan *et al.* 1999; McGeoch & Gaston 2000; Cronin 2003; Urbas *et al.* 2007; Ewers *et al.* 2013). Nevertheless, these cross-habitat differences in food-web structure, combined with reciprocal spillover of organisms between adjacent habitats (Rand *et al.* 2006; Lucey & Hill 2012; Macfadyen & Muller 2013), strongly suggest that if some 'blending' of species interactions takes place in food webs at habitat edges, then they may be important for linking food webs in space, potentially due to consumers linking resources across habitats (McCann *et al.* 2005).

Here I take a quantitative food-web approach to determine how community composition and interaction structure re-assemble at the interface between natural and intensively-managed production habitats. I propose three hypothetical scenarios for how food webs at habitat edges ('edge webs') may be assembled from source populations of potentially-interacting species in the two adjacent habitats (Fig. 2.1). First, a '*non-stick*' edge web could occur if adjacent habitats do not share any species in common. The centre of the edge in this case would mark a clear division between the different habitat types in the composition of species and their interactions. However, this might be unrealistically restrictive as a 'null' hypothesis for the merging of food-web structure, given the known ubiquitous movement of generalist species across habitats (Rand *et al.* 2006). Hence, rather than the straw man of no species overlap, a more realistic expectation might be to have

significantly lower overlap in species and interaction composition across the edge than across sites within each of the habitats.

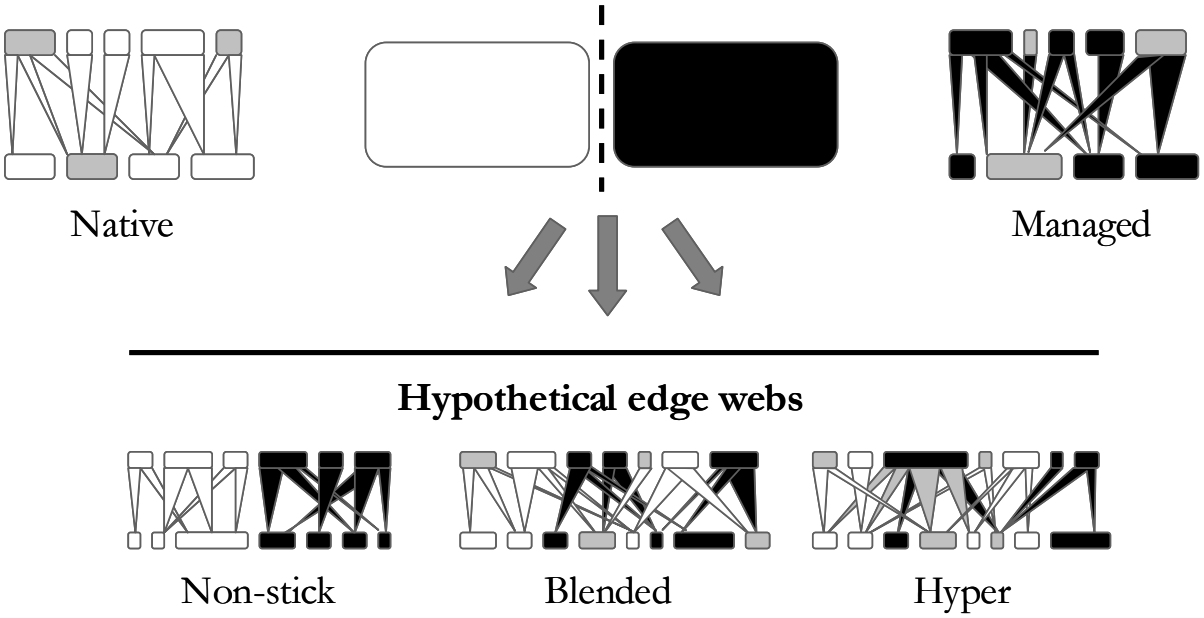

Figure 2.1: Schematic representation of the hypothetical webs formed at the interface of two habitats (in this example, one native and one managed). On each web, the bottom level bars indicate different resource species and the top level bars indicate consumer species, with the width of the bars representing species abundance. The lines between trophic levels indicate that those species are interacting, and the width of the lines represents the frequency of each trophic interaction. White represents species and interactions occurring in the native habitat, black those that occur in the managed habitat. Grey species co-occur in both habitat types and grey interactions (in the *'hyper'* web) represent new interactions. The dashed line between habitats delimits the centre of the edge. Below are three hypotheses for the merging of food webs at edges: the '*non-stick'* edge web represents the scenario whereby adjacent habitats do not share species; '*blended'* webs occur when edge webs are formed by a mixture of interactions from the two habitats and their frequencies are proportional to those in the adjacent habitats; '*hyper'* webs occur when interactions at the edge occur at different proportions than those of the adjacent areas and/or there are new interactions occurring at the edge that do not occur in either the managed or native habitat.

As an alternative hypothesis, a '*blended*' edge web could occur if reciprocal spillover of species across the habitat interface is high, such that the structure of an edge web is no different from the combination of the adjacent habitat webs. In this scenario, the combination of interactions at the edge would be a random sample of species and interactions from the adjacent habitats, with the frequency of each interaction potentially (though not necessarily)

being proportionate to that in the two adjacent interior habitats. The structure of the *'blended*' edge web would thus be predictable by knowing the interactions that occur in each adjacent habitat.

The third potential scenario, a '*hyper*' web, could occur if the mixing of species across the edge interface results in novel interactions or alters the frequency of existing interactions compared with those observed in the adjacent habitats. For example, consumers might reach higher densities by exploiting complementary resources from adjacent habitats, and this could increase their consumption/impacts on resource species at the edge (Duelli *et al.* 1990; Tylianakis *et al.* 2004; Rand *et al.* 2006). In the '*hyper*' web scenario, named for its analogy to the 'hyperdynamism' observed for some processes at edges (Laurance *et al.* 2006; Leidner *et al.* 2010), edge webs would have similar species composition to the adjacent habitat interiors, but the interactions and their frequency of occurrence (interaction strengths) might be quite different. Such effects could arise due to the differential responses of different organisms to habitat edges (Ewers & Didham 2008), altered abundance of consumers or resources due to spillover (Rand *et al.* 2006), altered abiotic conditions at edges (Didham & Lawton 1999; Ewers & Banks-Leite 2013), and/or the formation of novel interactions (Fagan *et al.* 1999) due to the mixing of new species or changes in conditions that facilitate potential interactions (Lovejoy *et al.* 1989; Summers & Underhill 1996).

To test these hypotheses, I quantified feeding interactions (links) between individual herbivores (Lepidoptera) and their parasitoids across large-scale edge gradients from remnant native forest into exotic plantation forests in New Zealand. Parasitism and herbivory are common ecological processes in both natural and managed systems, making these ubiquitous food webs one of the most common model systems for quantifying terrestrial antagonistic interaction networks (Memmott *et al.* 1994; Albrecht *et al.* 2007; Tylianakis *et al.* 2007; Kaartinen & Roslin 2011). Parasitoids also play a crucial role in the control of pests, such

that they are considered by some to be the most important biological control agents in agriculture (Mills & Wajnberg 2008; Pennisi 2010). I use community-wide changes in quantitative species interaction networks, to demonstrate that habitat edges affect the assembly of interactions within a community, and produce novel food-web structures that could not be predicted simply by combining webs from adjacent habitats.

2.3 Methods

2.3.1 Study region

The Nelson and Marlborough area (South Island, New Zealand) was originally covered by native southern beech (*Nothofagus spp.*, Fagaceae) forest from the coast to the alpine tree-limit. However, conversion to agriculture, plantation forestry and urbanization have greatly reduced the area of natural forest, and edges have proliferated (Ewers *et al.* 2006). Exotic plantation species are used for timber, and commercial forestry is increasingly concentrated on a single species: *Pinus radiata*. Nowadays, juxtaposition of native and production forests is common in this region and worldwide.

For this study I selected eight sites (172°47'E to 173°53'E and 41°12'S to 41°33'S) where it was possible to establish a large-scale (ca. 1 km) edge gradient from natural beech forest into exotic plantation forest. All the plantation forests chosen were closed-canopy monocultures of *Pinus radiata*, 19-26 years old. The minimum distance between sites was 2.7 km (maximum distance 94.6 km), i.e. nearly three times the distance between sampling plots within an edge gradient.

2.3.2 Sampling

Sampling was conducted in a split-plot design at each of the eight sites. Each site consisted of an edge between native beech forest and adjacent pine plantation (Fig. S2.1), with the centre of the edge zone considered to be the last row of pine trees of the plantation forest. The pair of adjacent forest types (native vs. plantation) represent the whole-plot scale in the design and each contained two nested subplots: an edge (10 m from the centre of the edge zone towards the forest interior) and an interior (400-500 m from centre of the edge zone), giving 32 subplots in total (four per site) (Fig. S2.1). Interior subplots were a minimum of 400-500 m from any other edge of the forest patch, to ensure that other edges adjacent to different habitats did not confound our treatments.

At each site, we sampled one 50 x 2 m transect (parallel to the edge) in each subplot (Fig. S2.2). All the transects within a site fell within an elevation range of 100 m to avoid potential confounding effects caused by altitudinal differences within sites (De Sassi *et al.* 2012), even though elevation varied from 70 – 637 m across sites. Sampling was repeated once per month from December 2009 to February 2010, and from October 2010 to February 2011.

Along each transect, all plants up to a height of 2 m were beaten with a 1 m long PVC pipe to dislodge insect herbivores. White collecting sheets (1 x 1 m^2) were placed under the plants prior to beating, and dislodged Lepidoptera larvae (caterpillars) were collected from these. Each plant species was beaten over a separate sheet in order to determine the plant species from which each herbivore was collected. In addition, at 5 m intervals along each transect (i.e., at 10 sampling points) the canopy of the nearest accessible tree was sampled by using a 9 m pole pruner to cut subcanopy branches, which were then beaten over the sheets.

To minimize the reduction of herbivore numbers over consecutive sampling rounds, each transect was moved 1 m away from that sampled during the previous month, such that the same plants were not sampled on multiple rounds. To better quantify the number of interactions between herbivores and parasitoids (that is, to make webs more representative of the diverse interactions occurring at a site), extra plants in sites for which the total number of herbivores collected was less than fifty were sampled. These samples were taken as close to the transect as possible, and used to increase the sample size of herbivores and parasitoids that emerged from them.

Herbivores were taken to the lab, identified to species or mophospecies (hereafter "species") and reared individually (in separate containers) under ambient conditions (16 C°, relative humidity of 60% and a light rhythm of 16L:8D). They were fed with leaves of the plant species from which they had been collected, plus a general Lepidoptera growth medium ('beet army worm diet' from Bio-Serv, Custom Research Diets and Environmental Enrichment Products, New Jersey, USA), until they either developed into adults or parasitoids emerged. Parasitoids were identified morphologically after their emergence, and where necessary, males (which in some genera cannot be identified to species level using morphology) were identified using molecular techniques. For molecular identification, I sequenced a region of the mitochondrial cytochrome C oxidase subunit I (COI) used in previous studies for parasitoid identification (Kaartinen *et al.* 2010), and related male sequences to those of female specimens that had been identified morphologically. Specimens for which sequences had a 97 % or higher similarity were considered to be the same species, as this captured most of the species defined without molecular means (Smith *et al*. 2013). For the morphospecies, both hosts and parasitoids were at least identified up to genus level according to current taxonomic classification (with the exception of Lepidoptera Pshychidae family for which only two species could be identified and the remaining four specimens

could not be assigned to a species and were lumped into the morphospecies 'Psychidae sp.'). A list of the plant, herbivore and parasitoid species involved in this study, and locations where voucher specimens have been deposited, can be found in Appendix 2.2 (Table S2.1).

To estimate the plant biomass sampled, I counted the number of leaves from each plant species that were beaten on each transect, and then multiplied this number by the average leaf mass per species. To calculate an average leaf mass (dry weight) per species, I weighed between 30-60 leaves of each plant species (depending on how variable they were in size). For 14 out of 99 species sampled, I estimated their weights based on the leaf weights of other species of similar leaf size (13 of them within the same genus), because of their scarce presence at the locations sampled. To obtain dry weight of leaves, foliage was dried in a drying oven at 60 C° for two weeks.

2.3.3 Analysis

For analyses I pooled monthly sampling periods into a single dataset for each of the 32 subplots, because individual sampling dates were not independent replicates of locations (edge vs. interior) or forest types (native vs. plantation), and also because sample sizes on each date were insufficient to allow robust time-series analysis. In addition to testing for changes in the species (parasitoid or herbivore) composition of edge communities, I also tested for changes in the interaction composition (*sensu* Laliberte & Tylianakis 2010). I defined each interaction as a parasitoid-host combination (a given parasitoid species attacking a given host species), and the frequency of each interaction could then be treated analogously to the abundance of each species in analyses. Thus, interaction composition was defined as the suite of different parasitoid-host combinations, and the relative abundance of interactions was defined as their respective frequencies.

2.3.3.1 'Non-stick' edge web hypothesis

To test whether edge webs might conform to a strict '*non-stick'* pattern, I compared herbivore community composition, parasitoid community composition, and the composition of herbivore-parasitoid interactions between edge and interior locations and forest types. If the edge food webs were *'non-stick'*, community compositions in the different forest types would not overlap (there would be no shared species).

However, given that some generalist species are known to occur in both forest types (Dugdale 1958; Milligan 1974; Berndt *et al.* 2006), I also tested a less strict definition of the '*non-stick'* web hypothesis. To do this, I compared the overlap of species and interaction composition among interior and edge communities from a single forest type against the overlap among adjacent edge webs sampled on opposite sides of the center of the edge (i.e. in different forest types). If species and interaction overlap within forest types was equal to or lower than that across different forest types at the edge, I would reject the *'non-stick'* hypothesis. Otherwise, if species and interaction overlap was higher within forest type, it would suggest that the edge marks a division between natural and managed habitat webs.

To compare herbivore, parasitoid and interaction compositions between forest types and edge vs. interior locations within forest, and to thereby test the *'non-stick'* hypothesis, I used split-plot Permutational Multivariate Analyses of Variance (PERMANOVA) (Anderson *et al.* 2008), based on two community dissimilarity measures, as recommended by Anderson *et al.* (2006). I used Jaccard and Hellinger dissimilarity measures because they differ in the emphasis they give to species composition vs. relative abundance (Jaccard incorporates only presence-absence of species/interactions, whereas Hellinger also incorporates relative abundances). The response variables (each measured with both dissimilarity measures) were therefore 1) dissimilarity in community composition of herbivores, 2) dissimilarity in

community composition of parasitoids and 3) dissimilarity in the composition of herbivore-parasitoid interactions. I fitted four-factor models, in which I entered site (random), forest type (fixed), plot (random), location (edge vs. interior; fixed) and the interaction between forest type and location as terms, with Type I (sequential) sums of squares (see Appendix 2.3 for more details on the PERMANOVA analyses). I also made pair-wise comparisons between edge vs. interior locations within each forest type.

Given that the forest types selected for this study were mostly formed by different plant species (Appendix 2.4, Fig. S2.6, Table S2.11), I tested whether differences in herbivore and parasitoid species composition and interaction composition held true after taking into account differences in the composition of plants sampled. This allowed me to determine whether there were factors, other than plant composition, affecting the composition of the upper trophic levels. I did this by including plant composition, the first axis of a principal coordinate analysis (PCO), as a covariate. By running each model twice, with plant composition first introduced as the last term in the models and then as the first term (using Type I/sequential SS) I was able to determine how the significance of other variables in the model changed after removing variation explained by plant composition. I used a Jaccard plant composition PCO axis for the herbivore, parasitoid and herbivore-parasitoid interaction PERMANOVA Jaccard models, and a Hellinger plant PCO axis for the models using Hellinger dissimilarity.

I also determined the distances of each observation to the centroid (observations being the herbivore, parasitoid and interaction community compositions of each site) and tested whether these distances differed between forest types, locations (edge vs. interior), and forest-location combinations. This allowed me to resolve whether observed differences in community composition across habitats could arise from differences in the variability of community composition between forest types, locations (edge vs. interior) or forest-location

combinations (Warton *et al.* 2012). To accomplish this, I used the Permutational Analysis of Multivariate Dispersions (PERMDISP) (Anderson 2006). I conducted all the permutation tests in the PRIMER v6 / PERMANOVA+ environment (Anderson *et al.* 2008), with P values for the statistics (pseudo-F values) based on 9,999 permutations.

In order to complete the assessment of the *'non-stick'* hypothesis I measured the degree of species and interaction overlap among subplots within forest types, and among adjacent edge webs (sampled on opposite sides of the centre of the edge). According to the most relaxed interpretation of the *'non-stick'* hypothesis, edge sites should be more similar to their respective habitat interiors than to the adjacent edge in a different habitat type. Given that the Jaccard and Hellinger indices represent compositional overlap among assemblages, I used them to compare species (herbivore and parasitoid combined, to be more conservative) and herbivore-parasitoid interaction compositions between native-interior vs. native-edge (NINE) assemblages, plantation-interior vs. plantation-edge (PIPE) assemblages, and native-edge vs. plantation-edge (NEPE) assemblages at each site, using an analysis of variance (ANOVA) approach. I entered compositional overlap as the response variable, habitat comparisons as the predictor factor (with NINE, PIPE, NEPE as levels), and site as a blocking factor. I tested the normality and homoscedasticity assumptions and log transformed species overlap estimated with Hellinger index in order to fulfil the assumptions. I used the aov function of the R environment version 2.15.1 (R Core Team 2012). Lack of significant differences between factor levels would not support the *'non-stick'* hypothesis, i.e. the edge does not mark a clear division between forest types.

2.3.3.2 'Blended' vs. 'hyper' edge web hypotheses

If the *'non-stick'* hypothesis was rejected, I hypothesized that the composition of edge webs would be determined by the simple combination of adjacent web assemblages from interior native and interior plantation forests. If that were the case, then the structure of edge webs could be predicted by randomly sampling interactions from the interior native and interior plantation forests (*'blended'* web). Alternatively, the edge web could contain interactions or species compositions that are absent from the interior of either habitat, and thereby exhibit a novel (*'hyper'*) structure. Given that the species composition and structure of food webs can respond differently to fragmentation (e.g., composition can change while food-web structure remains constant; Kaartinen & Roslin 2011), I analyzed these two components separately.

First, to test whether community composition at forest edges was a mixture of species from the interior areas, I pooled webs from the adjacent native and plantation edges to form one combined 'empirical edge web' for each site, and compared it with a pooled 'interior metaweb' formed by the native interior and plantation forest interior webs combined. This analysis investigated whether or not species and interactions (and also their relative abundances/frequencies observed at edges) overlapped with those observed in the two interior habitats. I compared the herbivore, parasitoid and herbivore-parasitoid interaction composition of the empirical edge webs vs. interior metawebs using PERMANOVAs as described above, but in this case the model only included site as a random factor and location (edge vs. interior) as a fixed factor to test whether species or interaction composition at edges differed from those of their respective interiors. As noted previously, I separated the effects of presence-absence from those including abundance or frequency by calculating Jaccard and Hellinger distance metrics.

Second, I took a further step to determine whether the structure of the empirical edge food webs could be predicted from the interior metawebs. From the empirical edge herbivore-parasitoid interactions, I constructed food webs (as above, two adjacent edge locations combined into one empirical edge web per site) and defined its structure by using quantitative food-web metrics (connectance, generality, vulnerability, link density, interaction evenness and number of compartments), which take into account species abundances and the strength of each trophic interaction (Bersier *et al.* 2002; Tylianakis *et al.* 2007) (see Appendix 2.5 for more details on the metrics selected). These metrics were calculated using the 'networklevel' function in the Bipartite package (Dormann *et al.* 2008) for R. I then compared the structure of empirical edge webs to simulated webs (hereafter 'null webs') generated by randomly subsampling from their respective interior metawebs at each site.

To conduct the null model simulations, I generated a set of random webs for each site by selecting interactions from the interior metawebs of each site using the 'mgen' randomization algorithm in the netstat function in R (Vázquez *et al.* 2009), which allows interactions to be selected according to a probability matrix. I used two probability functions to generate the random (null) webs: the 'homogeneous probability model' and the 'heterogeneous probability model'. In the 'homogeneous probability model', all the interactions that occurred in the interior metaweb had the same probability of being selected to occur in the null webs. This model has the advantage that it does not assume that interactions that occur frequently in the forest interiors are also frequent or more likely to occur at the edge. However, species are not all equally abundant, so even if individuals of those species interacted at random, then a typical log-normal species-abundance distribution could generate non-random patterns in numbers and frequencies of interactions, i.e. food-web structure (Vazquez *et al.* 2007). For example, species with higher abundance would be more

likely to interact with many other species and to thus appear more connected in the web. This could predispose the empirical edge webs to appear different from the null webs. The selection of quantitative web metrics minimises sampling biases (Banasek-Richter *et al.* 2004) and therefore partly mitigates this problem, but I nevertheless used a second null model to fully account for this possibility.

In the more constrained 'heterogeneous probability model', the probability of an interaction from the interior metaweb being selected was proportional to its frequency of occurrence in the interior habitats. The resulting null networks should have a more realistic distribution of interaction numbers (i.e. 'degree') and frequencies, because these are derived from the distribution of interaction frequencies observed in the interior habitats. Therefore, the homogeneous model randomly selected interactions, whereas in the heterogeneous model, interactions that were frequent in the interior habitats had a higher chance of being selected in the null edge webs.

When generating the two sets of null models, I constrained the null webs to have the same number of interactions (parasitism events) as found in the empirical edge webs (for each site), so that differences in food-web structure between empirical and null webs would not be an artefact of differences in the number of parasitism events observed in the interior metawebs. The models did not constrain the number of species, because species richness did not differ significantly between empirical edges and interior metawebs (Z-value = -0.48, P = 0.628) (Appendix 2.6, Fig. S2.7). Repeated assignment of interactions (parasitism events) to the same pair of species generated the frequencies of each interaction, such that null webs were quantitative with weighted links between species.

Each of the null models generated a set of 9,999 null webs per sampled web (9,999 permutations in all the randomizations) and calculated their quantitative food-web metrics,

returning the mean and confidence interval of metric values for each null web. I then compared the empirical edge web metrics with those generated by the null models (for each site) and counted the number of empirical edge webs that differed significantly from the null expectations (i.e. that fell outside the 95% confidence interval of the null metric distribution). In order to plot standardised differences between empirical edge web metrics and their null expectations, I calculated Z scores by subtracting the mean null expectation of each metric from its corresponding empirical metric and dividing it by the standard deviation of the null distribution.

Because testing multiple empirical edge webs (one per site) against their respective null webs creates a cumulative risk of Type I error, I used a Bernoulli process to calculate the probability of each test being significant by chance alone, given the number of webs tested and the number of tests performed (Moran 2003):

$$p = [\ N!/(N-K)!K!\ ] \times \alpha^{K} (1-\alpha)^{N-K}$$

where N is the number of tests (16 in this case: 8 empirical edge webs, 2 tests for each to see if they were significantly higher or lower than expected under the null distribution) and K is the number of tests below α ($\alpha = 0.05$). A Bernoulli probability lower than α would suggest that the number of empirical webs that differed from their null expectations was unlikely to have arisen by chance.

If community composition of the empirical edge webs did not differ significantly from the composition of the interior metawebs, and there were no differences in web structure between the empirical webs and the null webs, then the edge food web would be considered to be a '*blended*' web. If only one null model differed from the empirical webs, it would give information regarding the ways in which the interactions at edges are selected from adjacent habitats (e.g. whether abundant interactions in interiors are more likely to

occur and be abundant at edges). Otherwise, if empirical edge webs differed from the expectation of both null models, they would be considered to represent a novel '*hyper*' web structure that was not predictable from the structure of webs in each habitat comprising the edge.

2.4 **Results**

2.4.1 Herbivore-parasitoid food webs

I sampled 99 different plant species, from which I collected and successfully reared 5,744 Lepidoptera individuals from 90 species (Table S2.1). From these herbivores, 719 parasitoids from 61 species emerged (Table S2.1). I constructed 32 herbivore-parasitoid food webs, which had an average connectance of 0.170 ± 0.048, and an average of 0.747 ± 0.104 links per species, similar to those found in other well-resolved food webs (Dunne *et al.* 2002).

2.4.2 'Non-stick' edge web hypothesis

I found significant differences in herbivore, parasitoid and herbivore-parasitoid interaction composition among forest types (Fig. S2.2), with metrics emphasizing both presence-absence alone (Jaccard) as well as the combined influence of differences in relative abundance and presence-absence (Hellinger) (Tables 2.1, S2.2). There was also a significant interaction effect between forest type and location (edge vs. interior) on the composition of herbivores, parasitoids and their trophic interactions. This was reflected in the higher similarity among herbivore communities in native interior forests compared to similarity

Table 2.1: Results of split-plot PERMANOVA analysis of Hellinger distance (with Type I sums of squares) of A) herbivore, B) parasitoid and C) interaction community composition across different forest types and locations (edge vs. interior). Plant composition was entered as a covariate last in the model. Bold values indicate significant results ($\alpha = 0.05$).

	Source	**df**	**SS**	**MS**	**Pseudo-F**	**P (perm)**
A) Herbivore composition	Site	7	2.991	0.427	2.017	**0.002**
	Forest type	1	1.470	1.470	6.944	**<0.001**
	Plot	7	1.482	0.212	1.239	0.135
	Location	1	0.332	0.332	1.940	0.065
	Forest type * Location	1	0.558	0.558	3.266	**0.002**
	Plant composition	1	0.246	0.246	1.439	0.163
	Residuals	13	2.222	0.171		
	Total	31	9.301			
B) Parasitoid composition	Site	7	5.965	0.852	1.657	**0.004**
	Forest type	1	1.497	1.497	2.911	**0.001**
	Plot	7	3.599	0.514	1.039	0.389
	Location	1	0.782	0.782	1.581	0.094
	Forest type * Location	1	1.049	1.049	2.121	**0.016**
	Plant composition	1	0.529	0.529	1.068	0.395
	Residuals	13	6.432	0.495		
	Total	31	19.853			
C) Interaction composition	Site	7	6.896	0.985	1.366	**0.036**
	Forest type	1	1.712	1.712	2.374	**0.004**
	Plot	7	5.048	0.721	0.945	0.695
	Location	1	0.990	0.990	1.299	0.180
	Forest type * Location	1	1.290	1.290	1.692	**0.040**
	Plant composition	1	0.648	0.648	0.849	0.658
	Residuals	13	9.913	0.762		
	Total	31	26.497			

among native forest edge communities, while the opposite pattern was observed at plantation forests (higher herbivore similarity among edge communities than interior communities). On

the other hand, parasitoid and interaction community composition were more similar in plantation interior forests than in plantation edges. Meanwhile, in the native forest, parasitoid and interaction community composition had higher similarity in the edge compared to the similarity among communities in the native forest interior. This interaction effect was significant when community similarity included relative abundances (Hellinger distance), but it was only significant for herbivore composition when a presence-absence measure (Jaccard) of similarity was used. This indicates that the edge/interior habitat differences applied more to relative abundances of parasitoid species and frequencies of interactions, rather than their presence or absence (Table 2.1). There was a tendency for herbivore composition to differ between the interior vs. edge locations in both forest types, while parasitoid composition only seem to differ between locations in the pine forest when community similarity included relative abundances (Jaccard) (Table S2.3).

When plant composition was entered first in the model (to determine whether observed differences in herbivores and parasitoids could be accounted for solely by differences in composition of the host plants sampled), this became the only significant factor affecting interaction composition in terms of presence/absence (Tables S2.4, S2.5), suggesting that habitat effects on communities were largely mediated by plant community changes. However, significant differences in the relative abundances of herbivore and parasitoid species (composition using Hellinger distance) at edges vs. interiors persisted after controlling for plant composition (Table S2.4), suggesting some direct effect of interior vs. edge locations on their relative abundances.

I did not find significant differences in homogeneity of multivariate dispersions for herbivores, parasitoids or their interactions, despite the significantly higher plant variability at edges than in interiors and in native than plantation forests (Table S2.6). This indicates that changes in community composition across forest types, locations (edge/interior) and the

forest type x location interaction, were not due to differences in the variability among levels of the factors.

Given that there was overlap in the composition of communities and interactions between forest types, I rejected a strict interpretation of the *'non-stick'* hypothesis. However, in order to completely reject it, I tested whether edges had species and interaction compositions that were more similar to their respective interiors than to the adjacent edge of the adjoining forest type. I found that the overlap in species compositions between assemblages within each forest type did not differ from the overlap among adjacent edges, i.e. native edge and pine edge, irrespective of whether I accounted for relative abundance of species or not (Hellinger: $F = 1.313$, $P = 0.291$; Jaccard: $F = 0.626$, $P = 0.545$ respectively), and neither did the overlap of species interactions (Hellinger: : $F = 1.648$, $P = 0.218$; Jaccard: $F = 1.187$, $P = 0.326$) (Table S2.7, Figs. 2.2, S2.3). Although assemblage composition differed across forest types, there was still as much overlap among adjacent edge webs (from different forest types) as there was between edge and interior webs within forest type. Hence, I rejected the *'non-stick'* hypothesis, since the centre of the habitat edge did not reflect a strict separation in species and interaction compositions among forest types.

2.4.3 'Blended' vs. 'hyper' edge web hypotheses

Herbivore, parasitoid and herbivore-parasitoid interaction composition of empirical edge webs did not differ significantly from that obtained by pooling the adjacent interior forest samples into interior metawebs (Fig. 2.3, Tables S2.8, S2.9). These results did not depend on the distance measure used (Hellinger vs. Jaccard), or change when including plant composition in the model (results not shown here).

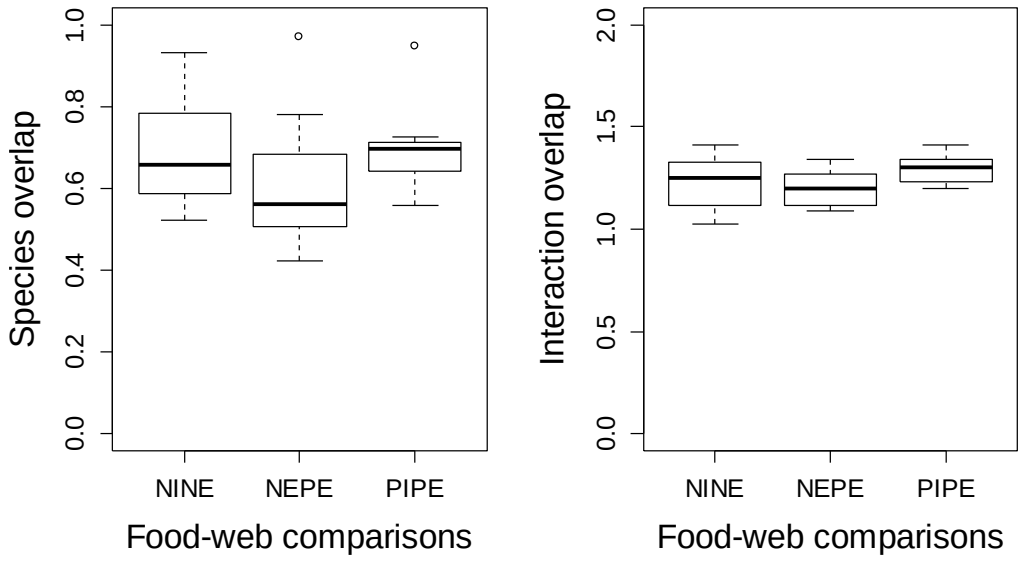

Figure 2.2: Species and interaction overlap (measured with Hellinger dissimilarity index) among interior and edge webs within native forest (NINE), between adjacent edges belonging to different forest types (NEPE) and among interior and edge webs within plantation forest (PIPE). There were no significant differences in the amount of overlap for each comparison, suggesting a lack of support for the non-stick hypothesis.

When comparing the structure of the empirical edge food webs with those generated by the null models (either by the homogeneous or heterogeneous probability models), I found that the empirical food-web metrics frequently differed significantly from null expectations (Figs. 2.4, S2.5). For the homogeneous probability model (Fig. S2.5), empirical values of vulnerability, link density and interaction evenness had a Bernoulli probability lower than 0.05 (Table S2.10), i.e. there was a very low probability that all the differences among empirical edge webs and null expectations would have arisen by chance. In contrast, only two out of eight edge webs differed from null expectation in their values of generality and number of compartments, and only one web differed from the connectance null expectations, which could plausibly have arisen by chance (Bernoulli probability > 0.05). These results were qualitatively similar for the heterogeneous probability model (Fig. 2.4), where all of the

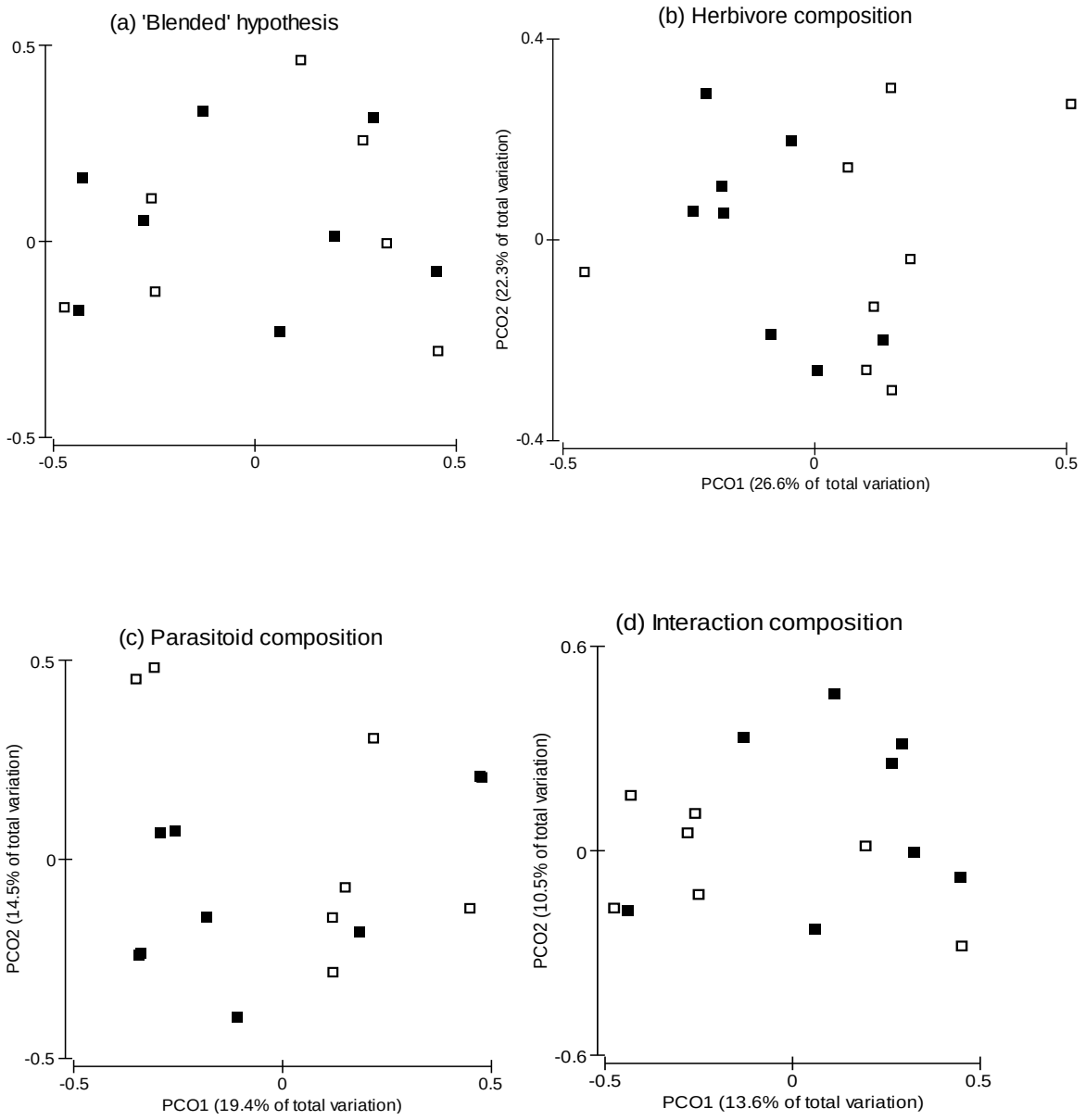

Figure 2.3: Principal Coordinate analyses (PCO) showing variation in (a) the expected composition of herbivores, parasitoids and their interactions, between edge vs. interior metawebs under the '*blended'* hypothesis, (b) the observed community composition of herbivores, (c) parasitoid community composition, and (d) the composition of herbivore-parasitoid interactions, based on a Hellinger distance metric. Open symbols indicate empirical edge webs, and solid symbols indicate interior metawebs.

food-web metrics evaluated, except for connectance and number of compartments, had more edge webs differing significantly from null expectation than would be expected by chance based on the number of tests conducted (Table S2.10).

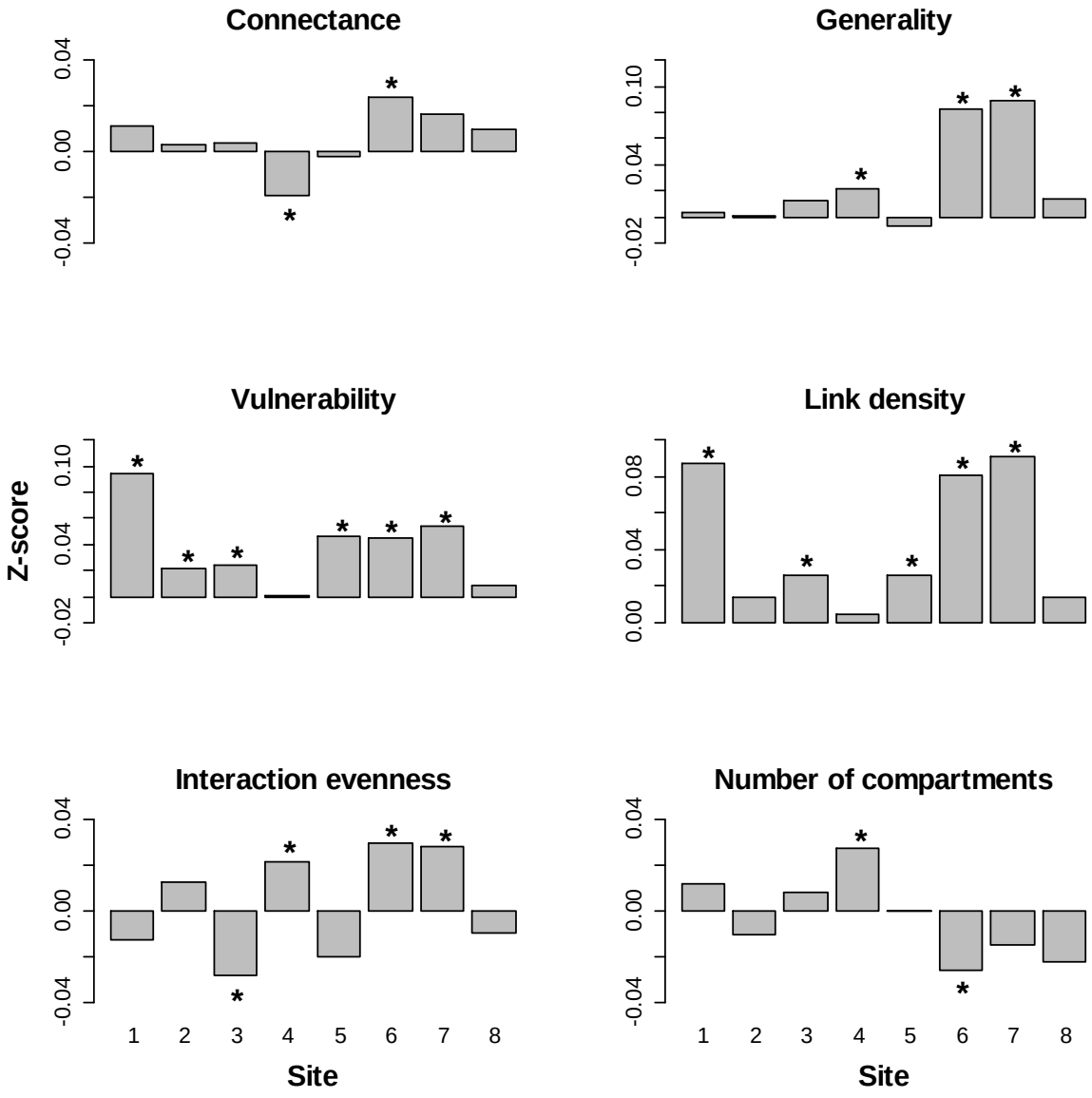

Figure 2.4: Standardised difference (Z score) between the empirical values of quantitative food-web metrics for edge food webs vs. the mean value of the null distribution for the heterogeneous probability model across the 8 sites. * = empirical value significantly different from the null expectation ($\alpha = 0.05$).

There was high overlap in composition of species and interactions between empirical edge webs and interior metawebs (pooled interior habitats), which suggests a certain degree of blending of community compositions from interior habitats. Nevertheless, the quantitative metrics for empirical edge webs could not be predicted by the structure of the interior metawebs. For example, edge webs tended to have more links per species (linkage density),

herbivores were attacked by more parasitoid species (vulnerability) and parasitoids tended to attack more herbivore species (generality) than expected (Fig 2.4, S2.5). I thus reject the '*blended*' web hypothesis in favour of the '*hyper'* web hypothesis.

2.5 **Discussion**

Although there is widespread evidence for the reciprocal spillover of prey and consumers between adjacent ecosystems (Rand & Louda 2006; Rand *et al.* 2006; Lucey & Hill 2012; Macfadyen & Muller 2013), the implications of this for species interactions have not previously been addressed beyond simple changes observed in pair-wise interactions (McGeoch & Gaston 2000; Urbas *et al.* 2007; Ewers *et al.* 2013). Here, I show that food webs of adjacent habitats do indeed overlap in composition to a significant degree at edges, but the resulting structure of the food webs cannot be predicted from a simple random draw of interactions from the adjacent interior habitats. Instead, edges exhibit a novel (*'hyper'*) web structure, with frequently higher than expected complexity (generality, vulnerability, and linkage density) at the interface of two habitats.

2.5.1 Community composition responses to different habitats and edges: the 'non-stick' hypothesis

The compositions of herbivore and parasitoid species and web interactions differed between native and plantation forests, as did herbivore composition between edge and interior locations. Such differences in community composition have been identified before when comparing natural vs. managed systems (Gardiner *et al.* 2003; Salvo *et al.* 2005; Grez *et al.* 2013), as well as in previous edge habitat studies (Ewers & Didham 2008), suggesting

that these types of alterations are quite widespread. The variation in herbivore, parasitoid and herbivore-parasitoid interaction compositions seemed to be primarily accounted for by differences in the plant communities available for herbivores, even though variation in the relative abundances of herbivore species could not be explained only by plant differences. For example, another factor accounting for variation in herbivore composition could be microclimatic differences (Bale *et al.* 2002). Overall, these findings suggest that bottom-up effects, in particular the availability of plant species across habitats, had strong impacts on upper trophic levels and their interactions.

Even though I found differences in herbivore, parasitoid and herbivore-parasitoid interaction compositions between native and plantation forests, the overlap of species and interactions across the edge was similar to the overlap across different locations within the same forest type. Hence, the centre of the edge did not represent a clear division in community composition of herbivores, parasitoids or their interactions among adjacent habitats, allowing for the rejection of the *'non-stick'* hypothesis.

2.5.2 Evaluating the evidence for food web assembly: the 'blended' and 'hyper' hypotheses

The *'blended'* edge hypothesis predicted that food-web composition and structure at habitat edges could be predicted from the combination of interior forest webs (interior metawebs). I found considerable blending of species composition and interactions at habitat edges, which was similar to previous findings of interior habitat species being found at edges (Ewers & Didham 2008). However, I could not predict the interaction structure of edge webs by simply combining the interactions of adjacent interior habitats. These findings illustrate that interaction web structure is not a direct consequence of species composition, as edge

webs had a predictable species composition, but an unexpected '*hyper*' structure. This also emphasises the importance of accounting for interaction structure in community studies, as these changes to the configuration of network interactions could have important consequences for the stability of the system as a whole (Thébault & Fontaine 2010).

2.5.3 Deviations from blended expectations: food-web structure at habitat edges

Some aspects of edge food-web structure deviated consistently from the null expectations across sites. Most of the metrics related to the extent to which species interact with other species, such as link density, generality and vulnerability tended to be higher than expected from the null models. This striking pattern suggests that habitat edges present larger numbers of trophic generalists than expected from composition of their adjacent areas, which is in concordance with the recent finding that specialist predators preferred interior habitats rather than edges (Wimp *et al.* 2011). This also accords with the 'specialization-disturbance' hypothesis (Vázquez & Simberloff 2002), which states that generalist species should benefit from fragmentation because they can exploit resources in multiple habitats, while specialists tend to rely on fewer resources, which makes them more vulnerable to habitat alteration. Previous studies in which other components of habitat fragmentation were analysed (Steffan-Dewenter & Tscharntke 2000; Krauss *et al.* 2003; Rand & Tscharntke 2007; Devictor *et al.* 2008; Cagnolo *et al.* 2009; Clavel *et al.* 2011) also found that generalist species were less vulnerable than specialists.

Higher vulnerability, generality and linkage density in empirical edge webs compared with their null expectations suggest that species at edges interact more frequently, and hence they should link network compartments (modules), including the networks of the two

adjacing habitats (Olesen *et al.* 2007). Consequently, I expected to find fewer compartments at edges, i.e. few specialized herbivore-parasitoid interactions (Wimp *et al.* 2011), though I did not find any such pattern. I also did not find differences in connectance between edge webs and null webs, potentially due to the null model features. In these models, I constrained the number of interactions in the null webs, to be the same as the number of interactions in the edge webs, and also the number of species did not differ significantly between the empirical edge webs and the interior metawebs, i.e. the size of the edge and null webs were similar. Given that both of these factors, contribute to connectance (Bersier *et al.* 2002), they could be explaining the lack of differences between edge and null webs.

Another component of food webs is the similarity of interaction strengths within webs (i.e. interaction evenness), which informs about the energy flow within web and hence is fundamental to understanding their stability (McCann *et al.* 1998). The contrasting patterns observed for interaction evenness between the two null models can be explained by differences in the result of each null model. In the homogeneous model, interactions from native and plantation interior forests were selected at random with equal probability. This increased the probability of obtaining null webs with all interactions having similar strengths, thus increasing the probability that empirical webs would have comparatively lower evenness, as observed. By contrast, the heterogeneous model selected interactions according to their frequency of ocurrence in the interior forests, leading to lower average evenness in the null webs. Empirical edge webs had higher interaction evenness than expected under this heterogeneous model, which could be related to the fact that each herbivore species was attacked by more parasitoid species. Since each herbivore species biomass would be consumed by several parasitoid species, the energy flow within an edge web would be more evenly distributed along the different pathways, rather than concentrated along single trophic interaction, as observed in other modified habitats (Tylianakis *et al.* 2007). Higher interaction

evenness has been related to ecosystem stability (McCann 2000; Tylianakis *et al.* 2010), which suggests that habitat edge food webs could be more stable than expected.

2.5.4 Conclusions

Species and interactions differ in their susceptibility to habitat edge characteristics (Laurance 2002; Ewers & Didham 2008; Ries & Sisk 2010). Here I have shown that, even though the species composition of edge food webs could be predicted from those of their adjacent areas, the configuration of interactions into network structure is not a direct consequence of the species composition. Rather, known processes such as reduced survivorship of certain species at edges (McGeoch & Gaston 2000), release from resource limitation (Urbas *et al.* 2007), susceptibility to microclimatic changes (Valladares *et al.* 2006), use by generalists of resources from multiple habitats (Rand & Louda 2006), and differential spillover of species across habitats (Rand *et al.* 2006; Macfadyen & Muller 2013), can affect species interactions and shape the structure of edge food webs in unpredictable ways.

There is urgent need to assess the responses of whole interacting communities to habitat fragmentation (Memmott 2009; Hagen *et al.* 2012). Ecologists have already begun to uncover the potential factors that could alter interaction networks in fragmented habitats, which include habitat modification (Tylianakis *et al.* 2007) and loss (Melián & Bascompte 2002; Fortuna & Bascompte 2006), patch size (Cagnolo *et al.* 2009; Aizen *et al.* 2012; Valladares *et al.* 2012), and isolation (Albrecht *et al.* 2007; Kaartinen & Roslin 2011). However, one of the main advances of landscape ecology has been the recognition that natural habitats are not simply islands floating in a hostile matrix, as assumed by island biogeography and metapopulation theory, but rather, they exchange species with the

surrounding matrix (Ricketts 2001; Blitzer *et al.* 2012; Tscharntke *et al.* 2012b). These cross-habitat flows may be important determinants of food-web structure (Polis *et al.* 1997; Huxel & McCann 1998; Tscharntke *et al.* 2012b), and as shown here, the exchange of species across edges might affect how food webs are assembled non-randomly from the species and interactions present in adjacent habitats. If we are ever to understand how food webs are structured at the scale of entire landscapes (McCann & Rooney 2009), it is crucial to understand how the juxtaposition of habitats affects species movement in both directions, and how this affects food-web topology in an increasingly fragmented world.

Chapter III

Phylogenetic diversity and coevolutionary signal among trophic levels change across a habitat edge gradient

3.1 Abstract

Incorporation of the evolutionary history of species assemblages into ecological studies allows for a better understanding of community composition, ecosystem functioning and responses to environmental changes. This approach might partly explain the impact of fragmentation and land-use change on assemblages of interacting organisms and even inform about potential cascading effects across trophic levels. Even where well-resolved phylogenies are not available for poorly-known faunas, it is still possible to estimate phylogeny with taxonomic distances.

Here, I used taxonomic distances and information on plant-herbivore-parasitoid feeding interactions (food webs) to study the effects of one of the most pervasive features of fragmented landscapes: habitat edges. Specifically, I asked how phylogenetic diversity of different trophic levels changes across an edge gradient between native and plantation forests, and how differences in phylogenetic diversity relate across trophic levels. I also tested whether the coevolutionary signal (i.e. congruence of consumer-resource phylogenies) among interacting species changed across the edge gradient.

I found that phylogenetic diversity responds differently across different trophic levels to differences in forest type. I observed marked changes in plant phylogenetic diversity across habitats, mostly driven by the presence of alien species, and higher phylogenetic variability in herbivore communities in interior native forests than in habitat edges and interior plantation forests. I did not find evidence of related herbivore species feeding on related plant species, potentially due to the high trophic generality of herbivores. However, related parasitoid species tended to feed on related herbivore species, suggesting the presence of coevolutionary signal among these organisms. Moreover, this coevolutionary signal was stronger in plantation forests, potentially due to reduction in the ability of parasitoids to attack hosts other than those with which they have best evolved to deal.

Overall, changes in land use from native to plantation forests differentially affected phylogenetic diversity across trophic levels, and it may also exert a strong selective pressure for particular coevolved herbivore-parasitoid interactions.

3.2 Introduction

Over the past decade, ecologists have increasingly been using information on the shared evolutionary history (i.e. phylogeny) of species to help understand patterns in the distribution and abundance of organisms (Webb *et al.* 2002; Mouquet *et al.* 2012). Phylogenetic hypotheses about taxonomic groups have the benefit of combining phenotypic information with past evolutionary events (Cadotte *et al.* 2010b; Srivastava *et al.* 2012). Furthermore, in combination with information on contemporary ecology, they provide a promising opportunity for improving our understanding of the mechanisms driving community structure (Cavender-Bares *et al.* 2009; Mouquet *et al.* 2012).

Phylogenetic diversity (i.e. phylogenetic distance among species in a community) has been used as a descriptor of community composition, primarily in studies of plant communities. Plant phylogenetic diversity has been found to increase plant biomass (Cadotte *et al.* 2008; Cadotte *et al.* 2009; Connolly *et al.* 2011; Flynn *et al.* 2011) via its role in increasing the complementarity of niches within the trophic level. Plant phylogenetic diversity has also been shown to relate positively with species richness of herbivores and predatory arthropods, by providing more habitat niches and/or more plant biomass (Dinnage *et al.* 2012), and hence could potentially affect the phylogenetic diversity of the upper trophic levels (Rezende *et al.* 2007). Therefore, studying phylogenetic diversity across trophic levels could greatly enhance our understanding of how differences in phylogenetic structure in one trophic level could cascade to other trophic levels in a food web (Srivastava *et al.* 2012).

Understanding changes to phylogenetic diversity in space and across trophic levels may also inform conservation and protection of the evolutionary history of communities and ecosystems (Vane-Wright 1992; Rodrigues & Gaston 2002; Forest *et al.* 2007; Devictor *et al.* 2010; Winter *et al.* 2013). In fact, recent research has found that climate change and human disturbance can reduce the phylogenetic diversity of communities (Knapp *et al.* 2008; Willis *et al.* 2008; Dinnage 2009; Helmus *et al.* 2010), suggesting that anthropogenic changes might 'select' only certain closely-related species to survive (Srivastava *et al.* 2012). In this sense, phylogenetic diversity could be informative of current and future species extinctions in a community.

Phylogenetic diversity of a community can also be affected by the introduction of alien (non-indigenous) species (Cadotte *et al.* 2010a; Gerhold *et al.* 2011). This, combined with the bottom-up effects of plant phylogenetic diversity on higher trophic level diversity (Dinnage *et al.* 2012), suggests that phylogenetic approaches could help ecologists to predict the composition and distributional responses of interrelated communities to global change

(Lavergne *et al.* 2010; Mouquet *et al.* 2012). In a similar vein, the combination of phylogenetic diversity information with species interaction patterns could be used to predict cascading effects among species. For example, recent research has shown that genetically similar consumers are more prone to feed on genetically similar prey when facing warmer temperatures (Lavandero & Tylianakis 2013), suggesting that anthropogenic disturbances could affect the strength of coevolutionary pressures among species and hence drive prey resource specialization (Schemske *et al.* 2009; Lavandero & Tylianakis 2013).

Interaction patterns among species can also be combined with phylogenetic information to determine the extent to which interacting organisms occupy corresponding positions in their phylogenetic trees. This congruence among interacting species' phylogenies can be interpreted as the occurrence of associations among those species being non-random in terms of their relatedness, which can be used to infer the presence of a coevolutionary signal (Brooks 1979; Klassen 1992; Legendre *et al.* 2002). Coevolution has a long history of research (Ehrlich & Raven 1964; Janzen 1980; Thompson 1989; Thompson 2009), given its importance for predicting changes in an organism triggered by changes in other organisms. The presence of a coevolutionary signal in ecosystems can provide information not only about the evolutionary history of the system, but also about the potential cascading effects of changes in abundance of species within the food web, such as those occurring after species loss.

Even though the benefits of incorporating evolutionary information into ecological studies are clear, the ability to obtain high-resolution fully-resolved phylogenies represents a major challenge for many taxa in many regions of the world. In part, this is why there have been only few combined eco-evolutionary studies. However, it is possible to use other methods, such as taxonomic relatedness, as a limited proxy for phylogenetic structure,

allowing ecologists to use existing datasets to start unraveling questions involving species relatedness (Cagnolo *et al.* 2011; Srivastava *et al.* 2012).

I adopt this approach of using easily-available taxonomic information as a surrogate for phylognenetic relationships within plant, herbivore and parasitoid communities to evaluate how phylogenetic composition at different trophic levels is affected by one of the greatest drivers of biodiversity loss: habitat fragmentation (Sala *et al.* 2000). Specifically, I measure changes to phylogenetic relationships within quantitative plant-herbivore-parasitoid feeding networks across an edge gradient between native forest and exotic plantation forest, as edges are a key component to understanding how landscape structure influences communities in fragmented ecosystems (Ries *et al.* 2004). Furthermore, I test whether the proportion of interactions between species that occupy corresponding positions in their respective phylogenies (and hence potentially coevolved together) changes across habitats. I hypothesize that:

1) Phylogenetic diversity of plant communities will decrease across the gradient from native forest towards plantation forest, and this potential reduction in niche availability (Dinnage *et al.* 2012) will cascade up to the herbivore and parasitoid trophic levels, decreasing their phylogenetic diversity as well. Therefore, I hypothesize that phylogenetic diversity of consumers will be positively correlated with that of their resources.
2) Trophic interactions between plant and herbivore, and herbivore and parasitoid species will tend to be phylogenetically congruent, such that related consumer species feed on related resource species. This will occur because, when consumers specialize on different resources, interspecific competition is reduced and this facilitates coexistence (Levine & HilleRisLambers 2009).

3) Plantation forests of exotic tree species will tend to have fewer phylogenetically-congruent species interactions, i.e. interactions that have coevolved, than would the native forest. This pattern could arise because interactions among organisms in the native forest would have had more time to coevolve than interactions recently created between the indigenous and introduced alien species, such as trees in plantation forests. Similarly, interactions between alien and indigenous species could also occur in habitat edges. Moreover, because habitat edges can have more generalist species than interior habitats (Fagan *et al.* 1999; Wimp *et al.* 2011), this could also create a weaker signal of consumer-resource coevolution.

3.3 Methods

3.3.1 Study region and system

The study sites were located in the Nelson and Marlborough area, in New Zealand. The region is characterized by the presence of native southern beech (*Nothofagus spp.*, Fagaceae) forests and plantation forests (mostly exotic *Pinus radiata* plantations), so that edges between these two forest types are widespread in the area. I selected eight sites in the region, each formed by an edge gradient (ca. 1 km long) from native forest into pine plantation forest (see Chapter II: Study region section for more details on the study area).

I focused on the study of Lepidoptera larvae as herbivores because they can have a considerable impact on plant productivity (MacLean 1984; Straw 1996), and their taxonomic diversity is known to increase with plant phylogenetic diversity (Dinnage *et al.* 2012). At the same time, there has been strong predator-prey research focused on interactions between Lepidoptera larvae and their parasitoid consumers, as parasitoids can exert strong control

over pests (Mills & Wajnberg 2008; Pennisi 2010), which facilitates the study of potential cascading effects across trophic levels.

3.3.2 Sampling

I established four sampling plots per site (across the edge gradient): one in the native forest interior, one in the plantation forest interior and one at the edge of each forest type (Figs. S2.1, S2.2). The collection of caterpillars in the field, as well as the estimation of plant biomass sampled, were done following the sampling procedures explained in Chapter II: Sampling section.

After collection of caterpillars in the field, they were taken to the lab for rearing until they either became adults or parasitoids emerged. All specimens were identified to species or morphospecies. For the morphospecies (hereafter 'species') of Lepidoptera or their parasitoids, specimens were identified at least to genus level, according to current taxonomic classification, though some species are still undescribed. The only exception to this was the family Psychidae (Lepidoptera), for which only two species could be identified and the rest (four specimens) were lumped into a family-level morphospecies which was excluded from analyses to be consistent with other identifications (which were at least to the genus level), though their inclusion did not qualitatively affect the results. All identifications were made with the help of expert taxonomists (J. S. Dugdale for Lepidoptera and Tachinidae, J. Berry for Braconidae, Chalcididae and Eulophidae, R. Schnitzler for Ichneumonidae and Tachinidae). Specimens were identified based on their morphology, except for parasitoids, which were also identified using molecular barcoding when species level identification was not possible using only morphology. For more details on the species identification procedure see Chapter II: Sampling section. For a list of the species and families see Table S2.1.

3.3.3 Phylogeny estimated by taxonomic distance

I used taxonomic distance among species from the same trophic level in order to determine their phylogenetic relationships, as suggested by Poulin and Moulliot (Poulin & Mouillot 2003). For each trophic level (plant, herbivore, parasitoid), I constructed taxonomic trees of the species by considering the number of steps that separate them in the tree according to taxonomy. Steps were defined according to the available Linnean classification for each trophic level. Therefore, for the plant tree I considered division, class, order, family, genus and species as nodes; for the herbivore tree, superfamily, family, subfamily, genus and species, and for the parasitoid tree, order, suborder, superfamily, family, genus and species. I did not use the same nodes across trophic levels because they were lacking for some species, particularly some New Zealand endemic parasitoid species, which have not been fully assigned all the categories of the Linnean classification. Despite this, I was consistent in the use of nodes within trophic levels, therefore it should not bias the results.

Although taxonomic trees have the disadvantage of underestimating evolutionary differences compared with real phylogenies (Weiblen *et al.* 2006), they have the advantage of being easily used for any food web where species have been identified, and for taxa for which robust phylogenies are unavailable, such as many insects. Although more accurate plant phylogenies are available, I wanted to have comparable metrics of community phylogenetic diversity across the different trophic levels, so I used taxonomic trees as a proxy for phylogenetic trees for all the trophic levels (as in Cagnolo *et al*. 2011).

3.3.4 Phylogenetic diversity metrics

The phylogenetic information in a community can be summarized using metrics analogous to the traditional commonly-used measures of diversity, such as species richness and species evenness (Helmus *et al.* 2007; Schweiger *et al.* 2008; Cadotte *et al.* 2010b). Such phylogenetic measures of diversity have been proposed to be a more accurate representation than taxonomic diversity of community-trait and functional diversity (Srivastava *et al.* 2012).

In order to determine the phylogenetic community composition of plants, herbivores and parasitoids, I selected three metrics that merge species phylogenies with different aspects of community composition: phylogenetic species variability (PSV), phylogenetic species richness (PSR) and phylogenetic species evenness (PSE) (Helmus *et al.* 2007). These metrics assume that there is an unspecified trait shared by all the species in the phylogeny, which evolves neutrally at a fixed rate. Phylogenetic species variability (PSV) quantifies the variance of this hypothetical trait by combining phylogeny and species variability with community information (see Appendix 3.1 for more details on the metrics used). The higher the relatedness among species in a community, the lower the variance of this hypothetical trait, and PSV decreases towards zero. PSV equals 1 when all species in a community evolved independently (i.e. they are equally distant) from a common ancestor, a pattern also known as a 'star' phylogeny. This metric is particularly useful for comparing between habitat types because it is unbiased by differences in species richness or relative abundance.

Phylogenetic species richness (PSR), calculated by multiplying PSV by the number of species in the community, represents the species richness in the community once relatedness among species has been taken into account. Closely-related species contribute less to community diversity than distantly-related species, so PSR has lower values when species in a community are closely related. PSR is directly analogous to a weighted measure of species

richness, which is commonly used in community ecology, and its maximum value equals species richness when all species of the community are equally-distantly related.

The last metric chosen was phylogenetic species evenness (PSE), which incorporates species abundances into PSV, and is therefore a measure of both phylogenetic and species evenness. If all species have the same abundance, PSE equals PSV; if species were to evolve in the form of a 'star' phylogeny, PSE represents the evenness in species abundances, with PSE reaching its maximum value of 1 when all species have the same abundances (Helmus *et al.* 2007).

3.3.5 Analyses

3.3.5.1 Phylogenetic diversity of consumers and resources across a habitat edge gradient

In order to detect differences in the phylogenetic diversity at each trophic level across a habitat edge gradient, I analyzed data using generalized linear mixed-effects models (GLMMs), with the lmer function of the lme4 package (Bates *et al.* 2012) in the R 2.15.1 environment (R Core Team 2012). I used the phylogenetic diversity metrics of each trophic level (i.e. plant, herbivore and parasitoid PSV, PSR, and PSE), calculated with the psd function of the picante package (Kembel *et al.* 2010) for R, as response variables, and forest type (native vs. plantation), location (edge vs. interior) and their interaction as fixed predictors. I also incorporated sampling plot nested within site as random factors to account for the non-independence of samples within a site. I used a Gaussian error distribution, and log transformed plant-PSR, plant-PSE, herbivore-PSR, herbivore-PSE and parasitoid-PSE variables to improve normality and homoscedasticity of residuals. I began with a full model, which was then simplified by removing interactions then main effects until no further reduction in residual deviance was achieved, as measured by the Akaike Information

Criterion (AIC). Given that parasitoid species richness and abundance have been found to depend on the abundance of their host herbivores (Tylianakis *et al.* 2006; Fenoglio *et al.* 2012), I included herbivore abundance as a covariate in the parasitoid models to control for its effects (Gotelli & Colwell 2001). For the same reason, I included plant biomass sampled as a covariate in the herbivore models, even though it did not qualitatively affect the results. I used a Markov Chain Monte Carlo procedure for estimating p-values of the Gaussian models, with the pvals.fnc function from the languageR package (Baayen 2011).

3.3.5.2 Does phylogenetic diversity of consumers depend on the phylogenetic diversity of their resources?

As a means of determining whether the phylogenetic diversity of each consumer trophic level was related to the phylogenetic diversity of its resource (the trophic level immediately below), I also used GLMMs with a Gaussian error distribution. I used herbivore phylogenetic diversity metrics (PSV, PSR, PSE) as the response variables, and their corresponding plant phylogenetic metrics as the predictor (in separate GLMM models), with plant phylogenetic diversity metrics calculated from the entire pool of plant species sampled, including both indigenous and alien plant species (species were classified as alien if they were introduced into New Zealand by humans, deliberately or accidentally). Subsequently, I tested whether these effects were due to indigenous plant species variability by using the same herbivore phylogenetic diversity metrics as response variables, but plant phylogenetic metrics calculated only from the indigenous plant species pool as predictors. Herbivore phylogenetic metrics were calculated only from indigenous herbivore species, because the number of alien herbivores was very low (six specimens) and they were only located in a few sampling plots, so their impact on the community was too small to warrant the inclusion of

total herbivore (including alien) diversity metrics in separate GLMMs. Herbivore PSV and PSE were squared root-transformed and PSR was log transformed in order to achieve the normality and homoscedasticity assumptions.

I used the same approach to determine whether phylogenetic diversity metrics of parasitoids were related to those of herbivores. For this, I used parasitoid phylogenetic diversity metrics calculated from indigenous and alien parasitoid species (see Appendix 3.3 for more details on the indigenous vs. alien parasitoid species in New Zealand) as the response variables and their corresponding herbivore phylogenetic diversity metrics as the predictors. To determine whether herbivore phylogenetic diversity was related only to indigenous parasitoid phylogenetic diversity, I performed a second set of models. For these models I used parasitoid phylogenetic diversity metrics calculated solely from indigenous parasitoid species as the response variables, and their corresponding herbivore phylogenetic diversity metrics as the predictors. All the models (herbivore-plant and parasitoid-herbivore) included plot nested within site as random factors to account for the non-independence of samples.

Because the above analyses involved a large number of separate models to test related hypotheses about phylogenetic diversity of consumers being determined by that of their resource, there may have been an increased risk of Type I error. Therefore, to determine whether the number of tests I found to be significant could have arisen simply due to multiple testing (Type I error), I used a Bernoulli process (Moran 2003) to estimate the probability of the number of significant tests arising by chance, given the number of tests conducted. I performed this analysis for each trophic level, including all the tests performed on the different phylogenetic diversity metrics within the trophic level.

To better understand changes in phylogenetic diversity across the edge, and also to compare phylogenetic metrics with commonly used diversity metrics that do not include species relatedness information, I tested for differences in species richness and abundance of each trophic level across the habitat edge gradient. I used GLMMs with plant richness, plant biomass, herbivore richness, herbivore abundance, parasitoid richness and parasitism rates as response variables and the same predictors and random factors as explained above in all the models. For the species richness models, I included abundance of that trophic level (biomass for plants) as a covariate, to control for differences in the sample size. For testing herbivore abundance, I also included plant biomass as a covariate, and to test abundance of parasitoids, I used parasitism rates as the response variable because it weights the number of parasitoids by the number of herbivores collected. For all the species richness models I used a Poisson error distribution, for parasitism rates I used binomial errors, and for plant biomass a Gaussian error distribution with estimation of P-values by MCMC sampling. For the herbivore abundance model I used a negative binomial distribution because the equidispersion assumption of the Poisson model was not achieved (Zuur 2009). I checked for overdipersion in all the Poisson and binomial models and in order to fulfill the homoscedasticity and normality assumptions of the Gaussian model, I log transformed plant biomass.

3.3.5.3 Phylogenetic congruence among consumer-resource interactions

In order to determine whether related species of consumers feed on related resource species, I analyzed the degree of congruence in the phylogenies of interacting herbivores and plants, and interacting parasitoids and herbivores at the regional level (i.e. data from all sites pooled to maximize sample size). High congruence among phylogenies would mean that

more closely-related consumers feed on more closely-related resource species, and this has been interpreted as evidence of consumer-resource coevolution (Legendre *et al.* 2002). To accomplish this, I pooled all samples from the 32 sampling plots to form a regional dataset defined by trophic level, and used the ParaFit test (Legendre *et al.* 2002) from the ape package (Paradis *et al.* 2004) in R, to test the congruence among the phylogenies of consumer and resource trophic levels. I performed two ParaFit tests, one for plant-herbivore interactions and the other for herbivore-parasitoid interactions. The test included a phylogeny for each of the interacting trophic levels and a consumer x resource species interaction matrix, comprising the feeding interactions recorded in the samples. The use of taxonomic distances based on morphology instead of a true phylogeny does not invalidate the hypothesis test (Legendre *et al.* 2002).

The null hypothesis of the ParaFit test is that consumers utilize resource species randomly with respect to the resource phylogenetic tree, while the alternative hypothesis is that consumers and their resources occupy corresponding positions in their phylogenetic trees. To test this, the ParaFit test maps the principal components of the consumer and resource phylogenies onto adjacent sides of the presence/absence interaction matrix, to generate a fourth corner matrix (Legendre *et al.* 1997). A global statistic is then derived from the fourth corner matrix by using the sum of squares of the elements of the matrix, and its significance is tested by performing permutations of the resources associated with each consumer and creating a distribution of the statistic under permutation. The rejection of the null hypothesis indicates that interactions among trophic levels do not occur at random, but rather that they are phylogenetically correlated. P-values were obtained by randomization of the resource-consumer interactions (9,999 permutations).

3.3.5.4 Consumer-resource interactions with coevolutionary signal across habitats

Some consumer-resource interactions could make a stronger contribution to the congruence pattern among phylogenies, and hence have a stronger signal of coevolution than others. After first testing for overall congruence in the network, I then identified interactions that occur non-randomly with respect to phylogeny, i.e. those between species that occupy corresponding positions in the phylogenies and hence may be coevolved. To accomplish this, I used the ParaFitLink2 test (Legendre *et al.* 2002), which assesses the null hypothesis that each particular interaction between two species might have arisen by chance with respect to the phylogenetic structure of the interacting groups. Those interactions for which the null hypothesis is rejected are considered to have a signal of coevolution. I chose ParaFitLink2 because it has good power for detecting coevolutionary interactions in empirical cases, where a portion of the interactions might have coevolved but the others might be random (Legendre *et al.* 2002).

To test whether the proportion of these interactions with a coevolutionary signal differs across habitats, I used a GLMM with a binomial error distribution. I entered the proportion of total interactions (i.e. parasitism events) with coevolutionary signal as the response variable and forest type, location (edge/interior), and the forest type x location interaction as predictors. I also included host abundance as a covariate and plots nested within sites as random factors to account for their non-independence. Furthermore, I tested whether the proportion of unique consumer-resource links (i.e. identity of trophic interactions) with coevolutionary signal changed across habitats. Each unique trophic link was defined as the resource consumer combination that formed it (a given consumer species feeding on a given resource species). I used the same model as explained above, but instead used as a response variable the proportion of unique consumer-resource links that presented a

coevolutionary signal. For both models I checked for overdispersion and performed model selection as explained in the first section of analyses.

3.4 **Results**

Species richness only varied significantly across the edge gradient at the plant trophic level, and was lower in native forest interiors than in native edges, and lower in plantation forest edges than native forest edges (Table 3.1, Fig. 3.1). Also, plant biomass tended to be higher in plantation forests, although this difference was only marginally significant. In contrast, no differences were observed for herbivore or parasitoid species richness across edge vs. interior locations, nor was forest type retained in the best-fitting models for herbivore and parasitoid richness (Table 3.1, Fig. 3.1). For the upper trophic levels, I found that the abundance of herbivores tended to increase when moving from the native interior across the edge to the plantation interior. Specifically, herbivore abundance was significantly lower in interior native forests than in native edges and higher in plantation forest interiors than native edges, while no difference was observed between native vs. plantation edges (Table 3.1, Fig. 3.1). Finally, no significant changes in parasitism rates were detected across habitats (Table 3.1, Fig. 3.1). For a complete table with all species and families sampled see Table S2.1.

Table 3.1: Coefficient table from generalized linear mixed effects models to determine changes in the species richness and abundance of plants, herbivores and parasitoids across a habitat edge gradient. These are the results from the best-fitting models, which were simplified from a maximal model including forest type (native vs. plantation), location (edge vs. interior) and their interaction as fixed effects. All models included plot nested within site as random factors. For each species richness model, the respective abundance (biomass for plants) was incorporated as a covariate, to control for potential variation in abundance. For the herbivore abundance model, plant biomass was included as a covariate, while parasitoid abundance was tested as parasitism rates, to control for differences in the abundance of their resources. We used a Poisson distribution for all the species richness models (Z-values), Gaussian for log transformed plant biomass (t-value, P-values estimated by Markov Chain Monte Carlo procedure), negative binomial for herbivore abundance (Z-values) and binomial for parasitism rates (Z-value). Forest P = plantation; Location I = interior location. Bold values indicate significant results ($\alpha = 0.05$).

Response variable	**Predictors**	**Estimate± SE**	**Z-value**	**P-value**
Plant species richness	Intercept	3.250 ± 0.108	30.193	< **0.001**
	Forest P	-0.541 ± 0.117	-4.622	< **0.001**
	Location I	-0.165 ± 0.081	-2.043	**0.041**
Plant biomass	Intercept	10.881 ± 0.107	101.680	< **0.001**
	Forest P	0.293 ± 0.151	1.930	**0.057**
Herbivore species richness	Intercept	2.891 ± 0.116	24.944	< **0.001**
	Herbivore abundance	0.001 ± 0.001	1.067	0.286
	Location I	0.007 ± 0.079	0.087	0.931
Herbivore abundance	Intercept	5.090 ± 0.137	37.20	< **0.001**
	Plant biomass	6e-07 ± 2e-06	0.340	0.733
	Forest P	-0.056 ± 0.117	-0.480	0.632
	Location I	-0.219 ± 0.110	-2.000	**0.046**
	Forest P*Location I	0.604 ± 0.156	3.860	< **0.001**
Parasitoid species richness	Intercept	1.966 ± 0.126	15.599	< **0.001**
	Parasitoid abundance	0.013 ± 0.005	2.846	**0.004**
	Location I	0.129 ± 0.116	1.109	0.268
Parasitism rates	Intercept	-1.954 ± 0.110	-17.823	< **0.001**
	Forest P	0.042 ± 0.093	0.450	0.653
	Location I	-0.050 ± 0.081	-0.615	0.539

3.4.1 Phylogenetic diversity of consumers and resources across a habitat edge gradient

Plant phylogenetic variability (PSV) was significantly higher at the edge of native forest than in the native forest interior (Table 3.2, Fig. 3.2), and higher in the plantation interior forest compared with the native edge when considering both indigenous and alien species. However, when considering only the indigenous plant species, I found no significant difference in PSV between forest types (t-value = -1.540, P_{MCMC} = 0.148), nor was the edge vs. interior location term retained in the model (see Appendix 3.2, Table S3.2 and Fig. S3.2, for supplementary results on indigenous plant phylogenetic diversity). This suggests that the higher PSV at native edge and plantation interior habitats, might be due to the presence of distantly-related alien species, which increased PSV.

In contrast to PSV, plant phylogenetic species richness (PSR) was significantly higher in native forests than in plantation forests, both including (Table 3.2, Fig. 3.2) and excluding (t-value = -5.071, $P_{MCMC} < 0.001$) alien species (Table S3.1). Given that PSR is calculated as the product of PSV and species richness, the lower values of PSR obtained in plantation forest might be due predominantly to the lower richness in the plantation compared with the native forest. Plant phylogenetic species evenness (PSE) was significantly lower in the plantation forest edge and native forest interior compared with the native forest edge (Table 3.2, Fig. 3.2), only when including alien species. However, when only considering indigenous plant species, plantation forest PSE was significantly lower than native forest PSE (t-value = -2.691, P_{MCMC} = 0.016), and the edge vs. interior location term was not retained in the model (Table S3.1). This suggests that the abundance distribution of indigenous plants was more even in native forests than in plantation forests.

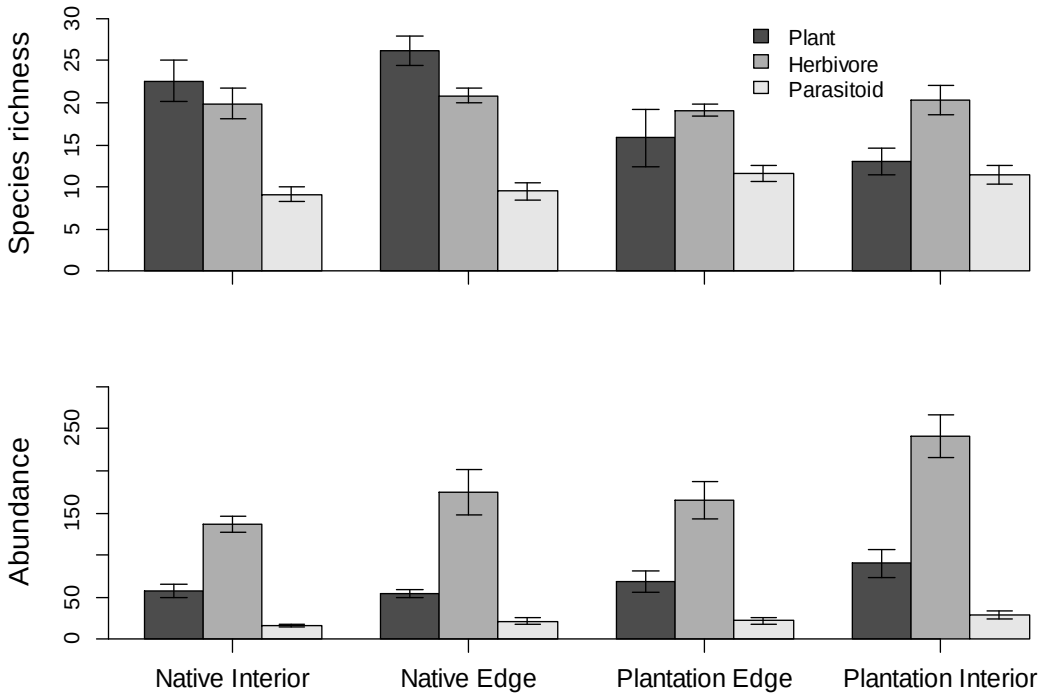

Figure 3.1: Mean (± SE) of species richness and abundance of plants, herbivores and parasitoids across a habitat edge gradient from native interior forest, to native forest side of the edge, plantation forest side of the edge and plantation interior forest. Plant abundance represents biomass sampled (Kg), while abundance of herbivores is the number of individuals collected, and of parasitoids, the number that emerged from herbivores.

For the second trophic level, the herbivores, PSV was significantly higher both in the native forest interior and plantation forest interior when compared with the native edge, while no significant differences were found between native vs. plantation edges (Table 3.2, Fig. 3.2). This suggests that interior forests harbour more differently related species than edges. Despite this, I did not find any differences in herbivore PSR across habitat types (Table 3.2, Fig. 3.2), probably because the change in PSV was masked by a lack of consistent variation in herbivore species richness. I found herbivore PSE to be lower in the interior plantation forests compared with the native edges (Table 3.2, Fig. 3.2), while no differences were found between native and plantation edges or edge vs. interior locations within the native forest.

Table 3.2: Coefficient table from generalized linear mixed effects models to determine changes in community phylogenetic diversity of different trophic levels across habitats (with a Gaussian error distribution, P-values estimated by Markov Chain Monte Carlo procedure). These are the results from the best-fitting models, which were simplified from a maximal model including forest type (native vs. plantation), location (edge vs. interior) and their interaction as fixed effects. All models included plot nested within site as random factors. The herbivore and parasitoid models included plant biomass and herbivore abundance respectively as a covariate in order to control for potential variation in resource abundance. Forest P = plantation forest; Location I = interior location. Bold values indicate significant results ($\alpha = 0.05$).

Trophic level	Phylogenetic diversity metric	Fixed effects	Estimate ± SE	t-value	PMCMC
Plant	PSV	Intercept	0.795 ± 0.011	69.190	**<0.001**
		Forest P	-0.013 ± 0.016	-0.810	0.427
		Location I	-0.036 ± 0.013	-2.800	**0.032**
		Forest*Location	0.056 ± 0.018	3.120	**0.022**
	PSR	Intercept	2.907 ± 0.113	25.615	**<0.001**
		Forest P	-0.580 ± 0.136	-4.278	**<0.001**
	PSE	Intercept	0.700 ± 0.036	19.221	**<0.001**
		Forest P	-0.235 ± 0.037	-6.377	**<0.001**
		Location I	-0.102 ± 0.037	-2.772	**0.015**
Herbivore	PSV	Intercept	0.843 ± 0.007	122.98	**<0.001**
		Forest P	0.017 ± 0.010	1.760	0.111
		Location I	0.037 ± 0.010	3.860	**<0.001**
		Forest*Location	-0.037 ± 0.014	-2.73	**0.014**
	PSR	Intercept	17.248 ± 1.309	13.174	**<0.001**
		Plant biomass	8e-07 ± 2e-05	0.047	0.739
		Forest P	-0.554 ± 1.026	-0.540	0.585
		Location I	0.476 ± 0.968	0.492	0.707
	PSE	Intercept	0.692 ± 0.037	18.763	**<0.001**
		Plant biomass	-2e-07 ± 4e-07	-0.563	0.549
		Forest P	0.036 ± 0.036	0.981	0.396
		Location I	0.041 ± 0.033	1.239	0.310
		Forest*Location	-0.154 ± 0.047	-3.258	**0.016**
Parasitoid	PVS	Intercept	0.628 ± 0.022	28.264	**<0.001**

	Location I	0.019 ± 0.024	0.779	0.521
PSR	Intercept	4.734 ± 0.933	5.073	<**0.001**
	Herbivore abundance	0.008 ± 0.005	1.692	0.087
	Forest P	1.034 ± 0.812	1.273	0.209
PSE	Intercept	-0.502 ± 0.088	-5.686	<**0.001**
	Herbivore abundance	-1e-3 ± 4e-4	-1.525	0.219
	Forest P	0.069 ± 0.078	0.874	0.351
	Location I	0.049 ± 0.047	1.025	0.448

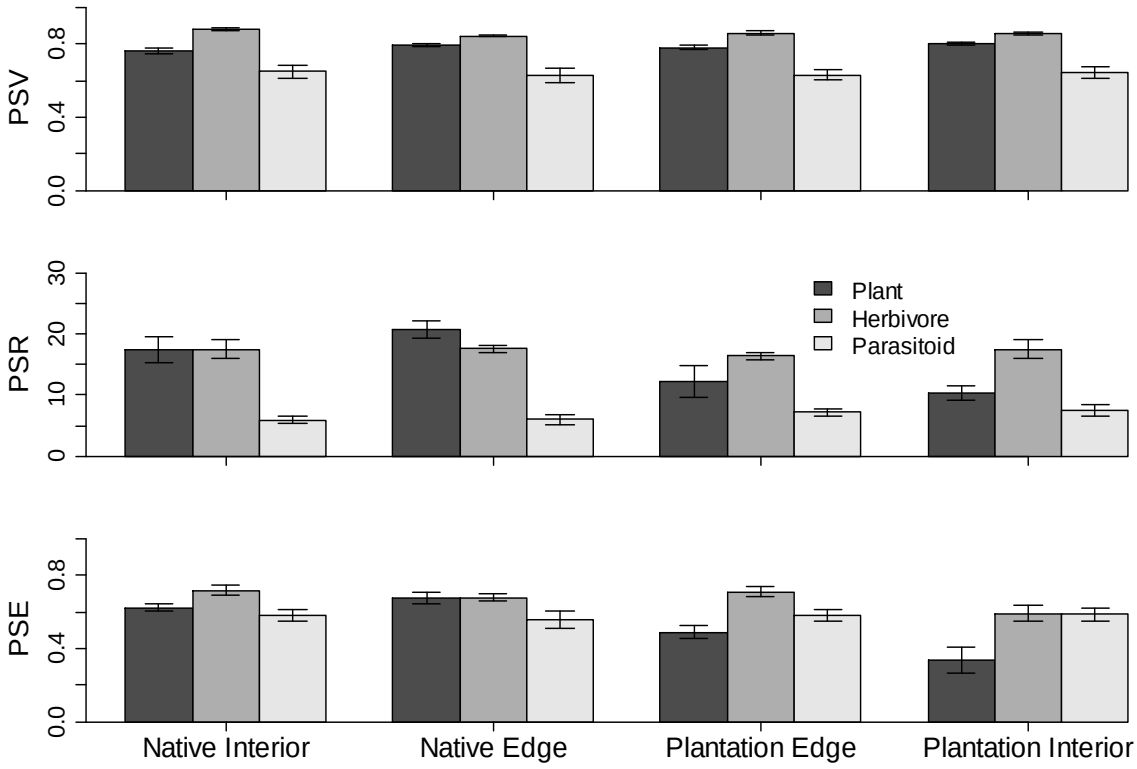

Figure 3.2: Mean (± SE) phylogenetic diversity of different trophic levels (plants, herbivores, parasitoids) across a habitat gradient from native forest interior, through native edge and plantation edge, to plantation forest interior. PSV = Phylogenetic species variability, PSR = Phylogenetic species richness, PSE = Phylogenetic species evenness.

This suggests that even though native habitats and plantation edges harbour fewer herbivore individuals, they nevertheless contain a wider phylogenetic variety of species with evenly distributed abundances.

For the upper trophic level, the parasitoids, no differences were found across forest types or locations (edge/interior) in PSV, PSR or PSE (Table 3.2, Fig. 3.2), even when non-indigenous parasitoids were excluded from the calculation of phylogenetic diversity (see Appendix 3.3, Table S3.2, Fig. S3.2 for supplementary results on indigenous parasitoid phylogenetic diversity).

3.4.2 Does phylogenetic diversity of consumers depend on the phylogenetic diversity of their resources?

I found a significant decrease in herbivore PSV with increasing plant phylogenetic diversity (Table 3.3A, Fig. 3.3). However, when restricting the analysis to indigenous plant species only, there was no longer any significant relationship observed between plant and herbivore PSV (Table 3.3B). Similarly, the significant increase in herbivore PSE with increasing plant PSE (Table 3.3A, Fig. 3.3) also seemed to depend on the presence of alien plant species (Table 3.3B). I did not find any significant relationship between herbivore and plant PSRs, either including (Table 3.3A, Fig. 3.3) or excluding (Table 3.3B) alien plant species. By contrast, parasitoid phylogenetic diversity metrics (PSV, PSR or PSE) were not significantly related to herbivore phylogenetic diversity (Table 3.3C), and these results did not change when considering only indigenous parasitoid species (Table 3.3D).

Table 3.3: Coefficient table from GLMMs for determining whether phylogenetic diversity of consumer trophic levels depends on the phylogenetic diversity of their resources (with a Gaussian error distribution and Markov Chain Monte Carlo procedure for estimating P-values). All models included plot nested within site as a random factor to account for the non-independence of samples. A) Plant phylogenetic diversity calculated with the entire pool of species present on each sampling plot, including indigenous and alien species. B) Plant phylogenetic diversity calculated only from indigenous plant species. C) Parasitoid phylogenetic diversity calculated from the entire pool of species (including indigenous and alien species). D) Parasitoid phylogenetic diversity calculated only from the indigenous species. Bold values indicate significant results ($\alpha = 0.05$).

	Response variable	**Fixed effects**	**Estimate ± SE**	**t-value**	**P_{MCMC}**
A)	Herbivore PSV	Intercept	1.084 ± 0.080	13.479	**<0.001**
		Plant (indigenous + alien) PSV	-0.284 ± 0.102	-2.774	**0.010**
	Herbivore PSR	Intercept	2.809 ± 0.083	33.82	**<0.001**
		Plant (indigenous + alien) PSR	0.002 ± 0.005	0.49	0.767
	Herbivore PSE	Intercept	0.525 ± 0.045	11.648	**<0.001**
		Plant (indigenous + alien) PSE	0.282 ± 0.079	3.561	**0.001**
B)	Herbivore PSV	Intercept	0.919 ± 0.036	25.440	**<0.001**
		Plant (indigenous) PSV	-0.077 ± 0.048	-1.615	0.128
	Herbivore PSR	Intercept	2.813 ± 0.071	39.66	**<0.001**
		Plant (indigenous) PSR	0.002 ± 0.004	0.56	0.708
	Herbivore PSE	Intercept	-0.364 ± 0.104	-3.489	**0.001**
		Plant (indigenous) PSE	-0.072 ± 0.181	-0.397	0.745
C)	Parasitoid (indigenous + alien) PSV	Intercept	0.187 ± 0.555	0.337	0.739
		Herbivore PSV	0.523 ± 0.642	0.814	0.430
	Parasitoid (indigenous + alien) PSR	Intercept	4.687 ± 1.951	2.402	**0.031**
		Herbivore PSR	0.116 ± 0.110	1.062	0.332
	Parasitoid (indigenous + alien) PSE	Intercept	0.524 ± 0.129	4.065	**0.001**
		Herbivore PSE	0.077 ± 0.189	0.407	0.732
D)	Parasitoid (indigenous) PSV	Intercept	1.548 ± 1.204	1.285	0.223
		Herbivore PSV	-0.989 ± 1.392	-0.710	0.509
	Parasitoid (indigenous) PSR	Intercept	2.888 ± 1.313	2.199	0.053
		Herbivore PSR	0.043 ± 0.073	0.586	0.624
	Parasitoid (indigenous) PSE	Intercept	0.485 ± 0.234	2.069	0.080
		Herbivore PSE	0.199 ± 0.345	0.578	0.497

For the plant and herbivore trophic levels, the probability of finding this number of significant tests by chance alone was P = 0.0006 and P << 0.0001, respectively. These suggest that it is unlikely that the significant results were all produced by a Type I error.

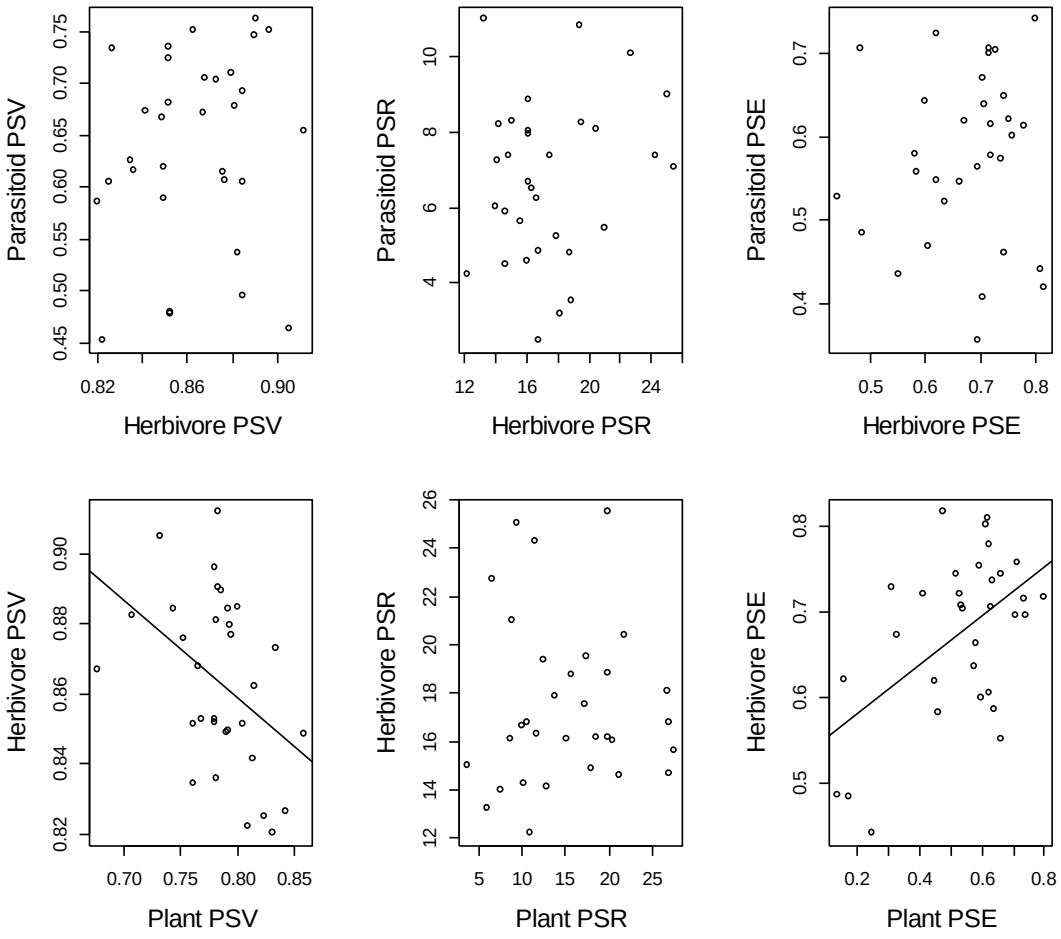

Figure 3.3: Relationship between parasitoid and herbivore phylogenetic diversity metrics and plant and herbivore phylogenetic diversity metrics. Plant and parasitoid phylogenetic diversity were calculated with both indigenous and alien species. PSV = phylogenetic species variability; PSR = phylogenetic species richness; PSE = phylogenetic species evenness. Continuous trend lines represent significant relationships: herbivore PSV vs. plant PSV t-value = -2.591, P = 0.017; herbivore PSE vs. plant PSE t-value = 3.561, P = 0.001.

3.4.3 Phylogenetic congruence among consumer-resource interactions and coevolutionary signal across habitats

I did not find evidence that closely-related herbivore species had the tendency to feed on closely-related plant species (P = 0.097), even when considering only indigenous plant and herbivore species (P = 0.179). Because this global test of congruence was not significant, only highly significant individual interactions should be considered for further testing changes in coevolutionary signal across a habitat edge (Legendre *et al.* 2002). Since none of the significant plant-herbivore interactions presented a sufficient level of significance (P > 0.010 in all cases), I did not explore further any individual interactions.

In contrast, at the upper levels of the food web I found evidence that more closely-related parasitoid species tended to attack more closely-related herbivore species (P = 0.018). I also found that the proportion of total interactions (i.e. parasitism events) with a coevolutionary signal among herbivore and parasitoid species was significantly greater in the plantation forest than in the native forest (Z = 2.220, P = 0.026) (Table 3.4A, Fig. 3.4A). Moreover, the proportion of unique herbivore-parasitoid links (i.e. interaction identities) that presented coevolutionary signal also was significantly higher in the plantation forest compared to the native forest (Z = 2.294, P = 0.021) (Table 3.4B, Fig. 3.4B).

3.5 **Discussion**

The high degree of global anthropogenic habitat alteration necessitates the urgent study of its effects on ecological and evolutionary relationships among species (Leimu *et al.* 2012). Here I found that plant and herbivore phylogenetic diversity changed across a habitat

Table 3.4: Results of GLMMs with binomial error distribution testing whether A) the proportion of herbivore-parasitoid interactions (i.e. parasitism events) with coevolutionary signal changed across forest types, and B) the proportion of herbivore-parasitoid interaction identities (i.e. links) with coevolutionary signal changed across forest types. Both models included host abundance as a covariate and plot nested within site as a random factor. Forest P = Plantation forest. Bold values indicate significant results ($\alpha = 0.05$).

	Response variable	Fixed effects	Estimate ± SE	Z-value	P
A)	Proportion of interactions with coevolutionary signal	Intercept	-2.477 ± 0.422	-5.874	<**0.001**
		Host abundance	0.006 ± 0.002	3.138	**0.002**
		Forest P	0.823 ± 0.371	2.220	**0.026**
B)	Proportion of interaction identities with coevolutionary signal	Intercept	-1.923 ± 0.371	-5.177	<**0.001**
		Host abundance	0.003 ± 0.002	1.986	**0.047**
		Forest P	0.530 ± 0.231	2.294	**0.022**

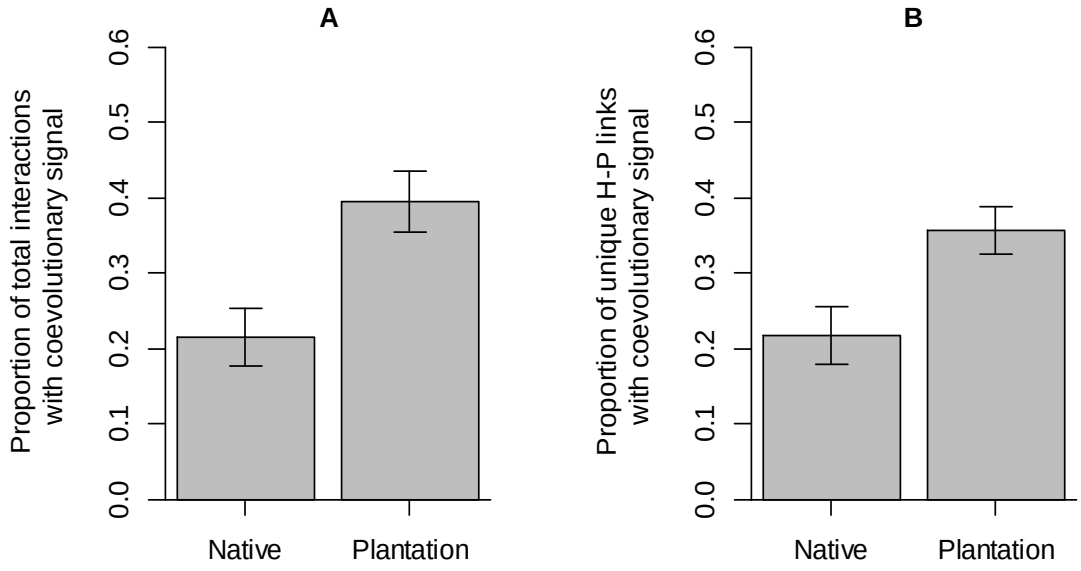

Figure 3.4: Mean (± SE) of the A) proportion of total interactions (i.e. parasitism events, N = 716) with coevolutionary signal, and B) proportion of unique herbivore-parasitoid links (i.e. identity of trophic interactions, N = 216) with coevolutionary signal, across forest types (native vs. plantation).

edge gradient between native vs. plantation forests, while parasitoids of the herbivores did not. Moreover, I found that herbivores seem to be more generalist in the resources they use,

contrary to the expectation that closely-related herbivores should feed on closely-related plants (Pellissier *et al.* 2013). Rather, I found high congruence in the phylogenies of interacting herbivore and parasitoid species. Even more, the parasitoid-host coevolutionary signal was stronger in the plantation forests, suggesting that anthropogenic changes affect parasitoid feeding preferences.

3.5.1 Plant-herbivore phylogenetic diversities across a habitat edge gradient

Trophic levels differed in how their phylogenetic diversity responded to the edge gradient. For the plant community, phylogenetic richness (PSR) and evenness (PSE) were lower in the plantation forests compared with the native forests, even when considering only indigenous species. This was not surprising, given that plantation forests were composed mainly of one planted species (*Pinus radiata* in this case) with some native plant species also colonizing and inhabiting plantations (Keenan *et al.* 1997; Newmaster *et al.* 2006). As noted by the values of PSR and PSE across forest types, the phylogenetically-weighted number of species was higher in the native forests and also the abundance of those species was more homogeneous in the native habitat. Although edge effects have been shown to affect plant composition in previous studies (Euskirchen *et al.* 2001), I did not find differences in the phylogenetic diversity of indigenous species between edge/interior habitat locations. This might be explained by the structural similarity of the edge/interior locations within forest type, which can affect microclimatic conditions and hence plant composition (Didham & Lawton 1999; Gehlhausen *et al.* 2000; Harper *et al.* 2005; Contreras *et al.* 2012).

In contrast to the other measures of phylogenetic diversity, I did not find differences in plant PSV across forest types when considering only indigenous species. This pattern

suggests that the indigenous lineages of plants that grow in the plantation forest are quite taxonomically broad, and that their colonization ability might not be related to phylogeny. This is potentially due to different lineages occupying different niches, as has been observed previously for plant species (Burns & Strauss 2010; Cadotte *et al.* 2012).

For the herbivore trophic level, PSV was substantially higher in the native forest interior. This suggests that even though plantation monoculture forests usually contain higher abundances of herbivores (Jactel *et al.* 2005), the native habitats harbour greater overall herbivore phylogenetic variability, i.e. species that are more distantly related. It could be possible that native habitats provide more or highly preferred adult feeding resources (such as nectar) and oviposition sites (Thompson & Pellmyr 1991; Schultz & Dlugosch 1999; Wäckers *et al.* 2007), which allow them to harbour a broader range of herbivore lineages, in contrast to plantation forests. Another potential explanation is that native habitats, with diverse plant assemblages, have more distantly related herbivores due to plant-herbivore coevolution (Pellissier *et al.* 2013). This led me to hypothesise that herbivore phylogenetic diversity would be related with plant phylogenetic diversity, which would be congruent with the relationship between plant diversity and herbivore species diversity (Siemann 1998; Hawkins & Porter 2003). However, I did not find any significant relationship between indigenous plant and herbivore phylogenetic diversities, potentially due to the low host specificity of Lepidoptera species in temperate forests (Dyer *et al.* 2007). Because herbivores tend to be more generalist (i.e. feed on different plant species) in this native temperate forest, higher diversity of plant lineages would not necessarily be related with higher diversity of herbivore lineages.

The absence of congruence among the plant and herbivore phylogenetic trees reinforced the idea that closely-related herbivore species do not necessarily feed on closely-related plant species, but rather that they are more generalist in the resource lineages they

use. This is also congruent with the herbivory pattern previously observed on other large persistent plants (Fox 1981), where each plant species was eaten by a large array of herbivores. Fox proposed the term 'diffuse herbivory', to refer to the damage imposed by the herbivore assemblage on this type of plant, and this should select for generalized plant defenses that affect a diverse consumer guild (Fox 1981). Such defenses should not impose strong selective pressures on the herbivores, because their short generation times relative to long-lived plants would facilitate counteradaptations. This suggests that plants respond to multiple herbivore species on both ecological and evolutionary time scales (i.e. diffuse coevolution; Janzen 1980; Fox 1981), rather than exhibiting pairwise coevolution, such that selection pressures exerted by a particular herbivore on a plant species are not affected by the presence/absence of other herbivore species (Hougen-Eitzman & Rausher 1994). Thus, it is not entirely surprising that I found no coevolutionary signal between plants and herbivores. It has been suggested that whether coevolution is pairwise or diffuse depends on the specialization degree of herbivores (Leimu & Koricheva 2006). Hence, it is possible that if the same study would be repeated in a tropical region, higher congruence among plant-herbivore phylogenies would be found, given the higher degree of specialization of herbivores in those regions (Dyer *et al.* 2007).

The presence of alien plant species can affect plant phylogenetic diversity (Cadotte *et al.* 2010a; Gerhold *et al.* 2011), potentially creating more arthropod feeding niches as well as increasing plant biomass (Connolly *et al.* 2011). Even though these changes have the potential to increase arthropod diversity (Dinnage *et al.* 2012), I found that plant phylogenetic variability (PSV) was negatively related to herbivore phylogenetic variability. It is possible that alien plant species, which contributed to this variability, benefitted only a few herbivore lineages, and hence the herbivore community phylogenetic variability decreased.

This hypothesis is supported by the numerous herbivore outbreaks in managed habitats driven mainly by one or few species (White 1974; MacLean 1984; Straw 1996).

3.5.2 Herbivore-parasitoid phylogenetic diversity and congruence across a habitat edge gradient

Changes in land use and habitat fragmentation are well known for increasing the frequency of habitat edges, and both have been shown to affect the species diversity of parasitoid communities (Tylianakis *et al.* 2005; Fenoglio *et al.* 2012). However, contrary to my expectations, parasitoid diversity did not change across the habitat edge gradient either with or without including relatedness among species. These differences can be explained by the type of habitat edge studied. Studies that analyse the effect of fragmentation usually use structurally contrasting habitats, such as forests vs. grasslands, or forests vs. crops (Tylianakis *et al.* 2005; Fenoglio *et al.* 2012; Macfadyen & Muller 2013), and these differences in vegetation structure can affect rates of parasitism (Menalled *et al.* 1999; Meiners & Obermaier 2004; Randlkofer *et al.* 2010). Hence, it is possible that I did not observe differences in parasitoid diversity because the vegetation structure across habitats did not change abruptly, and hence dispersal of parasitoid species was not significantly affected by the edge (Rand *et al.* 2006).

I also did not find any relationship among parasitoid and herbivore phylogenetic diversity at the site level, although at the regional level I observed significant congruence between herbivore and parasitoid phylogenies, suggesting that for such mobile predators and prey (van Nouhuys & Hanski 2002; Elzinga *et al.* 2007), a regional study may be necessary for detecting coevolutionary signals. Phylogenetic congruence among hosts and parasitoids can be understood from the life history of most of the parasitoids in this study. These

endoparasitoids have an intimate relationship with their hosts, because in their larval stage they live inside their hosts (Askew & Shaw 1986) and have to cope with their immune system (Vinson 1990). Therefore, close associations among host and parasitoid clades can be expected. Furthermore, because both hosts and parasitoids have similarly short generation times, this may increase the possibility of detecting coevolutionary changes (Bouletreau 1986).

Herbivore-parasitoid interactions that contributed most to the congruent pattern among herbivore and parasitoid phylogenies were found to be more abundant, and make up a greater proportion of all the interactions, in plantation forests than in native forests. This stronger coevolutionary signal in plantation forests suggests that parasitoids in the disturbed habitats may only cope with the hosts for which they have best evolved to deal. Reduction in parasitoid host-range has also been observed in higher-temperature habitats (Lavandero & Tylianakis 2013), suggesting that global environmental changes may be affecting predator plasticity to respond to novel pests.

3.5.3 Conclusions

Phylogenetic diversity changed across a habitat edge gradient, but not all trophic levels of a food web responded in the same predicted manner. Moreover, changes in phylogenetic diversity across habitats were mostly driven by the presence of alien species. I also found that congruence in the phylogenies of interacting plants and herbivores was not as strong as congruence among herbivores and parasitoids, potentially due to herbivores being more generalist in the resource lineages they consume. Moreover, herbivore and parasitoid interactions that presented a stronger coevolutionary signal (i.e. stronger congruence in their phylogenetic tree positions) were more abundant in managed habitats, suggesting that

modified habitats might exert strong selective pressure towards particular interactions. Overall, land-use change can alter not only species diversity, but also phylogenetic diversity and coevolution patterns among species, with potentially profound implications for ecosystem functioning and stability.

Chapter IV

Complementarity and redundancy of interactions enhance attack rates and spatial stability in host-parasitoid food webs

4.1 Abstract

Complementary resource use and redundancy of species that fulfil the same ecological role are two mechanisms that can respectively increase and stabilize process rates in ecosystems. For example, predator complementarity and redundancy can determine prey consumption rates and their stability, in some cases providing invaluable control over economically-damaging herbivore species. Even though multiple herbivores are usually attacked at different rates by multiple predators in a community, few studies have focused on these biodiversity mechanisms in entire herbivore-enemy assemblages, and even fewer take into account the pattern and relative frequency of feeding interactions within the community, which affect overall consumption rates.

Here, I used a quantitative food-web approach to study the community-wide effects of complementarity and redundancy of consumers (parasitoids) on herbivore control in temperate forests. By incorporating trophic interactions (links) among species as a proxy for energy flow among organisms, I tested the mechanisms driving the biodiversity-functioning relationship in diverse empirical multi-trophic communities.

I found that complementarity in host resource use by parasitoids was the strongest predictor of absolute parasitism rates at the community level, and that redundancy in host-use patterns stabilised community-wide parasitism rates in space, but not through time. These effects could potentially explain contradictory results previously obtained from predator diversity and ecosystem functioning research.

This study shows that known mechanisms underpinning predator diversity effects on both functioning and stability can easily be extended to an entire community, providing a link between biodiversity and food-web research.

4.2 Introduction

The relationship between biodiversity, ecosystem functioning and stability has a long history of research (May 1973; Montoya *et al.* 2003; Hooper *et al.* 2005; Gravel *et al.* 2011b; Fenoglio *et al.* 2012). Species diversity is usually positively related with rates of ecosystem functions (Hooper *et al.* 2005), and this relationship may be driven by a number of different underlying mechanisms. These include: i) "sampling effects" which result when a few species have strong effects and are more likely to be found in more diverse assemblages (Huston 1997; Wardle 1999; Loreau 2000); ii) "facilitation" resulting when positive interactions between species promote ecosystem functioning (Fowler 1986; Cardinale *et al.* 2002; Bruno *et al.* 2003); or iii) "resource complementarity" (also termed "niche partitioning") when differences in resource-use strategies and functional traits allow species to specialize on different resources, or on the same resource but in different locations or times (Hooper *et al.* 2005; Yachi & Loreau 2007; Richards & Schmidt 2010).

In addition to enhancing mean functional rates, biodiversity may affect variability in functioning, which is particularly important for services that are considered to benefit humans (Daily *et al.* 2000; Díaz *et al.* 2006; Daily *et al.* 2009; Sekercioglu 2010). The 'insurance hypothesis' predicts that increasing diversity should lead to more stable (i.e. less variable) ecosystem functions, due to multiple species being able to fill the same role and therefore maintain a function when other species decline in abundance (Walker 1992; Naeem & Li 1997). Asynchrony in population responses to the environment and redundancy of functional responses should enhance insurance effects, and thereby minimise variability in ecological functions (Yachi & Loreau 1999). Although initially applied to temporal variability, spatial insurance effects may also reduce site-to-site variability in attack rates (Loreau *et al.* 2003).

Although much of the initial work on biodiversity effects focused on the productivity of plant communities (Balvanera *et al.* 2006; Cardinale *et al.* 2006), a growing body of research has considered trophic interactions in a diversity-functioning context, thereby extending the multiple predator effects framework (Sih *et al.* 1998; Cardinale *et al.* 2003; Ives *et al.* 2005; Casula *et al.* 2006; Duffy *et al.* 2007; Finke & Snyder 2008) with important implications for biological control (Sih *et al.* 1998; Wilby & Thomas 2002; Cardinale *et al.* 2003; Straub *et al.* 2008; Snyder & Tylianakis 2012).

The effect of biodiversity on prey attack rates seems to depend on the trophic level at which diversity is being considered (Duffy 2002). For example, higher prey diversity has been related to lower predation rates (Montoya *et al.* 2003), while higher predator diversity has been related to increased predation (Ives *et al.* 2005; Tylianakis *et al.* 2006; Fenoglio *et al.* 2012). To add complexity, changes in predator diversity can also affect prey diversity (Chase *et al.* 2002), suggesting that the biodiversity within discrete trophic levels *per se* might not be the best way to explain changes in functioning of complex ecosystems.

Importantly, in multi-trophic systems, 'ecosystem functioning' seems to be the net result of interactions within and among trophic levels (Thompson *et al.* 2012) and not just interactions between individual species pairs (Tylianakis & Romo 2010; Wilby & Orwin 2013). Given that the cumulative effect of multiple predator species on their prey assemblage is determined by a complex array of factors at different trophic levels (Hillebrand & Cardinale 2004; Douglass *et al.* 2008; Wilby & Orwin 2013), it is important to extend knowledge beyond consumer-prey interaction pairs and move towards a deeper understanding of diversity-function relationships in multi-species trophic systems.

Despite the theoretical and applied relevance of understanding community-wide interactions among multiple prey and predator species, studies addressing biodiversity effects on predation have primarily considered assemblages that only contain between 2-6 predator species and seldom consider how the structure of predator-prey interactions might influence the outcome (Cardinale *et al.* 2003; Finke & Snyder 2008). A few exceptions that have extended the traditional biodiversity-functioning approach by considering not only the multiplicity of species, but also the pool of interactions among them, have found important effects of the strength (Rooney & McCann 2012) and number of interactions (Montoya *et al.* 2003; Thébault & Loreau 2003) on prey consumption. In fact, it has even been suggested that the link between biodiversity and ecosystem functioning may have more to do with how species interact, i.e. the structure of food webs, than how many species form the community (Montoya *et al.* 2003; Thompson *et al.* 2012). Therefore, in order to move forward in understanding these mechanisms, it is necessary to quantify biodiversity effects in the context of the food-web interactions that occur among predators and prey in the community.

By combining information on predator and prey diversity and composition with measures of energy flow and frequency of interactions, food webs provide a natural tool with which to examine the effects of biodiversity on ecosystem functioning and stability

(Thompson *et al.* 2012). This approach provides a more holistic view of consumer-resource interactions by incorporating direct and indirect effects of species on each other, thereby providing insights into species dynamics and consumption rates (Poisot *et al.* 2013). However, despite the clear potential link between trophic complexity (i.e. food-web structure) and predator complementarity effects (Thompson *et al.* 2012), there has been little research examining functional outcomes in a food-web context (Montoya *et al.* 2003; Macfadyen *et al.* 2009; Poisot *et al.* 2013). Beyond recent theoretical work suggesting the potential for effects of functional complementarity on ecosystem functioning (Poisot *et al.* 2013), complementarity and redundancy in empirical large-scale communities has received little attention, despite their potential for affecting not only functioning but also the stability of ecosystems.

One reason for this lack of research could be that determining the trophic niche of many species of generalist predators under field conditions can be logistically difficult. However, with relatively specialised predators such as parasitoids, it becomes easier to quantify complementarity in their trophic niche. Given that parasitoids make a strong contribution to the ecosystem service of pest control (Mills & Wajnberg 2008; Pennisi 2010), host-parasitoid communities provide avenues for developing and improving management strategies against herbivore pests.

Studies on host-parasitoid food webs have found parasitoid species richness to relate to increased parasitism rates and also temporal stability of parasitism (Cardinale *et al.* 2003; Tylianakis *et al.* 2006; Macfadyen *et al.* 2011; Fenoglio *et al.* 2012), while others have found no effect (Marino & Landis 1996; Menalled *et al.* 1999; Macfadyen *et al.* 2009). These conflicting results may not be surprising, as theory suggests that the strength of any predator diversity effect must depend on the extent to which different parasitoid species partition their host resources (Finke & Snyder 2008), which in turn depends on the diversity and

distribution of prey species (Tylianakis *et al.* 2008b; Tylianakis & Romo 2010; Wilby & Orwin 2013). Thus, to incorporate prey resource partitioning, the way in which consumer interactions are structured in a network could provide a link between predator and prey diversity, niche overlap and their joint impact on attack rates and their variability.

Moreover, functional complementarity might also influence species diversification through niche partitioning (Kozak & Wiens 2010), which could be reflected in the phylogenetic diversity of communities (i.e. a measure of relatedness among species in a community). If this is the case, then predator relatedness could be as informative as resource complementarity in explaining variation in attack rates, and at the same time would be considerably easier to measure (relatedness could be measured from samples of the predator community without needing to quantify links between predator species and their prey).

Here I use empirical host-parasitoid food webs from forests to test the following hypotheses:

1) Higher functional complementarity (i.e. host-resource partitioning among parasitoid species) will increase average parasitism rates across the entire community.
2) Resource overlap (redundancy) among parasitoid species that attack the same host species will provide insurance effects leading to lower variability (i.e. higher stability) of parasitism through time and space. In this sense, communities dominated by generalist parasitoid species should have more spatially- and temporally-stable attack rates than communities with fewer generalists.
3) Because niche partitioning promotes species coexistence and diversification as well as complementarity, I hypothesise that phylogenetic variability of parasitoids within a community will be positively correlated with functional complementarity in host use and, as a consequence, parasitism rates on hosts.

4.3 **Methods**

4.3.1 Study region

In the Nelson/Marlborough regions of New Zealand I sampled host-parasitoid food webs at eight different sites. Each site was composed by two adjacent forest types representative of the two predominant forest types in the region (native southern beech, i.e. Nothofagus sp., and exotic pine plantation). At each site, four sampling plots were established, with two in each forest type (Fig. S2.1). In total, therefore, I had 32 sampling plots, but given that the four plots from each site were non-independent, I nested sampling plots within sites in all the analyses (for more details on the study region and sampling design see Chapter II: Study region and Sampling sections). Even though there was high variability in food-web structure and absolute parasitism rates among sampling plots, there were no significant differences in structure or function (parasitism) between forest types or locations (edge vs. interior) of the sampling plots within forest types (Chapter III: Results section, Table 3.1), therefore I do not discuss habitat type differences here.

4.3.2 Sampling

In each sampling plot I collected Lepidoptera larvae (herbivores, hereafter also referred to as 'hosts') along a 50 x 2 m transect. I sampled each plot once per month from December-February (2009-2010) and November-February (2010-2011). After collection in the field, larvae were taken to the laboratory for rearing. For a more complete description of the sampling and rearing procedure see Chapter II: Sampling section.

4.3.3 Analyses

I used a quantitative food-web approach to link parasitoids with their hosts (Tylianakis *et al.* 2007), because food webs incorporate all the species and interactions within a community or subset of the community. By including the strength (in this case measured by the frequency) of trophic interactions as an estimate of energy flow, quantitative food webs are a good tool for testing questions pertaining to the biodiversity-function relationship (Thompson *et al.* 2012).

First, I tested the effects of functional complementarity on parasitism rates. I calculated cumulative parasitism rates (parasitism rates across the entire sampling period) for each sampling plot as the number of parasitoids that emerged divided by the total number of herbivore hosts collected over the total sampling period (hosts that died due to other reasons were not included in this denominator, as I could not be certain that these were not parasitized). I measured parasitoid functional complementarity as the total branch length of a functional dendrogram based on quantitative differences among parasitoid resource-use, i.e. hosts consumed (Devoto *et al.* 2012). To do this, I first created one matrix for each web, in which host species were represented as rows, parasitoid species as columns and the values within the cells represented the frequency with which each host-parasitoid interaction occurred. I then created a distance matrix among parasitoid species from each of the initial host-parasitoid matrices (using Euclidean distance), using the fd function of the Bipartite package (Dormann *et al.* 2008), for the R environment (R Core Team 2012). Values within the distance matrix represent the similarity among parasitoid species regarding the resources they shared. Then, from the distance matrix, parasitoid species were clustered according to their similarities in resource use, and a dendrogram was created, with distances among parasitoid species (branches of the dendrogram) equivalent to their similarity in resource use

(i.e. the longer the branch length among two parasitoid species, the fewer host resources they share). Finally, the total branch length of the dendrogram was calculated, which represents the value of functional complementarity of the web.

I tested the effect of parasitoid functional complementarity, as a fixed predictor, on cumulative parasitism rates as the response variable using a generalized linear mixed-effects model (GLMM), with a binomial error distribution. I included sampling plots nested within sites as random factors to control for the non-independence of plots within sites.

Because it is possible that host niche partitioning among parasitoids could also be associated with parasitoid speciation, communities with more distantly-related parasitoids might be expected to have the greatest complementarity. To test for this possibility, I included parasitoid phylogenetic species variability (PSV) (Helmus *et al.* 2007) as a predictor in the model, calculated with the psd function of the picante R package (Kembel *et al.* 2010). The phylogenetic species variability index can acquire values between 0-1, increasing towards 1 when species within a community are less phylogenetically related (for more details on the calculation of the phylogenetic species variability index see Chapter III, 3.3.3 Phylogeny estimated by taxonomic distance, 3.3.4 Phylogenetic diversity metrics, and Appendix 3.1).

Second, I tested the effect of redundancy on variability in parasitism rates in both space and time. Temporal variability in parasitism rates in each sampling plot across sampling months was estimated as the standard deviation in parasitism rates across months divided by the mean parasitism rate in that sampling plot, i.e. the coefficient of variation (CV) (Tylianakis *et al.* 2006). As a measure of spatial variability of parasitism rates across sites, I calculated the CV of parasitism rates among sampling plots within a site (standard deviation of parasitism rates across sampling plots within a site divided by the mean

parasitism rate in that site). I defined parasitoid functional redundancy as the weighted average number of parasitoid species attacking each host species, otherwise known as food web 'vulnerability' (Bersier *et al.* 2002), calculated at the sampling plot and at the site levels, using the networklevel function (Dormann 2009) from the R Bipartite package (Dormann *et al.* 2008). I used these two scales because multiple measures through time from the same plot allowed me to calculate within-plot temporal variability, whereas spatial (i.e. between-plot) variability could only be calculated at the site scale.

To evaluate the variability in parasitism rates through time, I used a GLMM with a Gaussian error distribution, and used the Markov Chain Monte Carlo (MCMC) resampling procedure to estimate P-values (Bolker 2009). I entered temporal variability of parasitism rates as the response variable, parasitoid redundancy (calculated at the sampling plot level) as the predictor and sampling plots nested within sites as random factors. To evaluate the variability in parasitism rates through space, I used a generalized linear model (with Gaussian error distribution), with spatial variability of parasitism rates entered as the response variable and parasitoid redundancy (calculated at the site level) as the predictor.

I also incorporated, in all the models, host species richness, parasitoid species richness and the weighted number of different interactions (i.e. links) divided by the number of possible links (quantitative connectance) (Bersier *et al.* 2002) as covariates, to test for effects of interaction structure on parasitism rates while controlling statistically for any differences in the number of species among webs, and the number of links between species. For a more detailed description of the connectance metric, see Appendix 4.3.

Each model included all the variables mentioned above, and was then simplified to the minimum adequate model by stepwise removal of fixed predictors until no further reduction in residual deviance (as measured by the Akaike Information Criteria, AIC) was

observed (Bolker 2009). I performed this model reduction process twice for each model, the first time without removing the covariates (parasitoid and host species richness and connectance), in order to determine whether complementarity and redundancy provided any information over and above the known effects of diversity. In the second iteration, by allowing removal of covariates I could test whether parasitoid complementarity and redundancy effects depended on the partial effects of the covariates. Also, because spatial variability was calculated at the site level, and consequently had low power (8 replicates = 7 d.f. total), allowing removal of covariates would reduce the probability of a Type II error, and hence detect potential effects that the full model with all the covariates might have not detected due to low power. Parameter estimates for fixed effects in the minimal models were tested for significance using a *Z*- or *t*-test (for binomial and Gaussian error distribution respectively) (Bolker 2009).

All the analyses were conducted in the R 2.15.1 environment (R Core Team 2012). I used the lme4 package (Bates *et al.* 2012) to carry out the GLMMs, and the languageR package, pvals.fnc function (Baayen 2011), for the MCMC procedure in Gaussian models. I tested for outliers, and two of our 32 webs exhibited strong leverage, one for complementarity and one for redundancy (Appendix 4.4, Fig. S4.3). I therefore removed these from all the analyses in order to avoid spurious trends, even though the results with or without the outliers did not change qualitatively. I also tested for overdispersion of residuals in the binomial model and normality and homoscedasticity in the Gaussian models, which required the temporal coefficient of variation of parasitism rates to be log transformed to meet model assumptions.

4.4 **Results**

Overall, I collected 5,743 Lepidoptera larvae with an average parasitism rate of 12.0 ± 3.6 % across sampling plots. Sampling plots had on average 8 ± 2 host species and 10 ± 3 parasitoid species, with mean parasitoid phylogenetic species variability of 0.636 ± 0.091.

After accounting for potential covariate effects of host species richness, parasitoid species richness and connectance, I still found that food webs with higher parasitoid functional complementarity had significantly higher cumulative parasitism rates ($Z = 2.238$, $P_{MCMC} = 0.025$) (Table S4.1A, Fig. 4.1A). This effect was not dependent on the partial effects of the covariates, as complementarity in resource use still increased parasitism rates significantly if the covariates were excluded from the model ($Z = 3.165$, $P_{MCMC} = 0.001$) (Table 4.1A). Surprisingly, neither species richness nor connectance had a significant effect on parasitism rates (Table S4.1A), and these were not even retained in the best-fitting model, when allowing for their removal (Table 4.1A). Moreover, parasitoid phylogenetic species variability was not correlated with parasitoid complementarity ($r = 0.32$, $P = 0.090$) (Fig. S4.1), nor retained in the best-fitting model, suggesting that having more different and distantly related species does not guarantee complementarity among parasitoids.

Contrary to my expectations, parasitoid functional redundancy did not affect temporal variability in parasitism rates (the coefficient of variation of parasitism rates through time), hence this term was removed from the best-fitting model with covariates (Table S4.1B, Fig. 4.1B). When allowing for covariate removal in the model selection procedure, parasitoid redundancy was retained in the best-fitting model, but still did not have a significant effect on

Table 4.1: Best-fitting model results, after allowing for removal of covariates (host species richness, parasitoid species richness and connectance), for models testing the effect of A) parasitoid functional complementarity on cumulative parasitism rates (with binomial error, Z-test); B) connectance and parasitoid redundancy on the temporal variation (coefficient of variation) of parasitism rates (with Gaussian error, t-value, p-values estimated by Markov Chain Monte Carlo procedure); C) parasitoid redundancy on spatial variation (coefficient of variation) of parasitism rates (with Gaussian error, t-value). Bold values indicate significant results ($\alpha = 0.05$). * = marginally significant result.

Response variable	**Fixed effects**	**Estimate ± SE**	**Z/t-value**	**P-value (P_{MCMC})**
A) Parasitism rates	Intercept	-2.471 ± 0.140	17.697	**>0.001**
	Parasitoid functional complementarity	0.017 ± 0.005	3.165	**0.001**
B) Temporal variability of parasitism rates	Intercept	-0.714 ± 0.223	-3.201	**0.037**
	Connectance	3.525 ± 1.021	3.453	**0.009**
	Parasitoid redundancy	-0.086 ± 0.059	-1.444	0.164
C) Spatial variability of parasitism rates	Intercept	0.372 ± 0.086	4.295	**0.005**
	Parasitoid redundancy	-0.051 ± 0.022	-2.361	*0.056

temporal variability of parasitism rates (Table 4.1B). In contrast, connectance was also retained in this best-fitting model, where it was significantly positively related to temporal variability in parasitism rates ($t = 3.453$, $P_{MCMC} = 0.009$) (Table 4.1B, Fig. S4.2). Connectance was also negatively correlated with parasitoid and host species richness ($r = -0.546$, $P = 0.002$ and $r = -0.668$, $P < 0.001$, respectively) but it was not correlated with parasitoid redundancy ($r = 0.343$, $P = 0.063$) (Fig. S4.1).

Spatial variability of parasitism rates showed a marginally significant decrease with increasing parasitoid redundancy ($t = -2.361$, $P = 0.056$) (Table 4.1C, Fig. 4.1C), although low statistical power for this model meant that this effect was only detected when allowing the removal of covariates in the model selection process. Nevertheless, spatial variability of parasitism rates more than doubled (from 0.104 to 0.278) across the observed range of parasitoid redundancy (from 2.589 to 5.392).

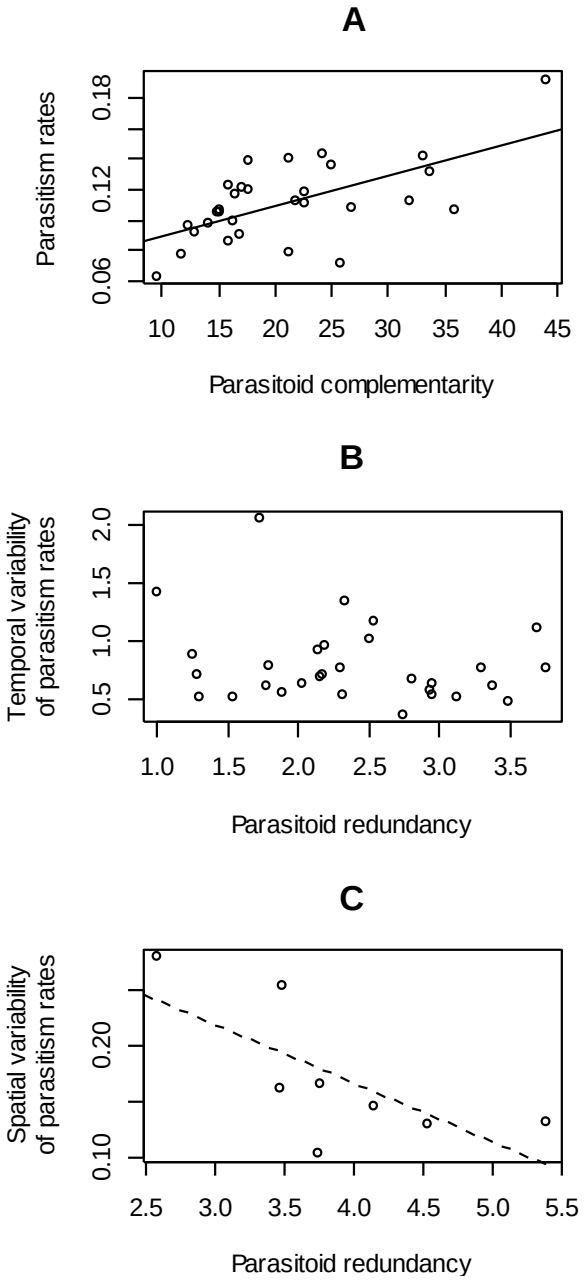

Figure 4.1: Relationship between A) cumulative parasitism rates (over the entire sampling period) and parasitoid functional complementarity; B) temporal variability of parasitism rates and parasitoid redundancy; C) spatial variability of parasitism rates and parasitoid redundancy. Although generalised linear mixed-effects models and generalised linear models were used to account for the non-independence of plots within sites (see Methods), the least-squares trend line is shown to illustrate the direction of effect. A solid line represents a significant relationship; a dashed line represents a marginally-significant relationship (P = 0.056).

4.5 **Discussion**

This study highlights the importance of considering the pattern of interactions among species in order to comprehend the mechanisms driving ecosystem functions and their stability, and even more, demonstrates the benefits of extending this approach to large-scale studies. I found that, at the community level, functional complementarity in host use among parasitoids was strongly associated with increased overall parasitism rates on hosts. Furthermore, the spatial stability (inverse of variability) of parasitism rates increased with parasitoid redundancy (i.e. host resource overlap), although no effect on temporal variability was detected.

Functional complementarity among parasitoids was a better predictor of community-wide parasitism rates than was species richness, connectance or phylogenetic diversity. This suggests that even though parasitoid species richness may positively influence parasitism rates (Cardinale *et al.* 2003; Fenoglio *et al.* 2012), the pattern of resource use among species is more important than richness *per se*, and it is a measure that can easily be extracted from food-web data. Moreover, even though phylogenetic diversity has been described as being superior to richness at representing the trait space in a community and, therefore, at explaining its functioning (Cadotte *et al.* 2008; Flynn *et al.* 2011; Srivastava *et al.* 2012), I found that phylogenetic diversity did not affect parasitism rates, nor was it correlated with parasitoid complementarity. Of course, it might be argued that the measure of phylogenetic diversity used here was based on taxonomic trees, which might underestimate differences among phylogenetic groups, and therefore true phylogenies could show different results (Devictor *et al.* 2010; Purschke *et al.* 2013). On the other hand, the results suggest that the commonly-used taxonomic classifications of species may not be an optimal measure of

complementarity among predators, and hence preserving diversity *per se* might not be enough to secure ecosystem services (Macfadyen *et al.* 2012).

Experiments examining the effects of niche partitioning among a small number of parasitoid species (Finke & Snyder 2008) found that increasing the number of specialist species (i.e. those with higher functional complementarity) increased parasitism rates, but increasing the number of generalist species did not have the same effect. This occurred because specialist species feed on different resources and therefore occupy complementary niches, such that when the number of specialists increases, new niches are occupied and hence parasitism rates increase. However, when the number of generalist species increases, their niches overlap and competition among species increases, mitigating any increase in parasitism rates. The congruence of those results with my community-wide finding of functional complementarity increasing parasitism rates, lends further support to the tenet that complementary resource use can be an important driver of ecosystem functioning in multi-trophic systems (Finke & Snyder 2008; Gravel *et al.* 2011a; Striebel *et al.* 2012; Poisot *et al.* 2013).

In contrast to the importance of functional complementarity as a determinant of cumulative parasitism rates, I found no support for the hypothesis that parasitoid redundancy (the average number of species attacking each host species, weighted by the frequency of each interaction) would stabilise temporal variation in parasitism rates in this study system. However, temporal variability in parasitism rates positively increased with food-web connectance. If we think about a community where species are highly connected, it could be expected that changes or fluctuations in the abundance of one species will affect several other species, and that this effect could easily cascade to other members of the web (May 1972; Melián & Bascompte 2002). Hence, highly-connected food webs might have more variable parasitism rates, such as those observed for temporal variability in this study. This might also

explain why in previous studies, increasing parasitoid diversity positively affected the temporal stability of parasitism rates (Tylianakis *et al.* 2006; Veddeler *et al.* 2010; Macfadyen *et al.* 2011), given that higher diversity decreases food-web connectance. Even though I did not observe a direct effect of parasitoid species richness on temporal variability of parasitism rates, richness was negatively correlated with connectance, which affected the temporal stability of parasitism rates.

The spatial variability of parasitism rates decreased with increasing parasitoid redundancy, in contrast to what I observed for the temporal component. Food webs are connected with one another at landscape scales (Leibold *et al.* 2004), and their connection by dispersal determines the spatial insurance of ecosystem functions (Loreau *et al.* 2003; Gonzalez *et al.* 2009). The stabilising effect of trophic redundancy across native and plantation forests bears important consequences for biological control of forest pests. Maintenance of adjacent natural habitats, local introduction or conservation of agents with generalist feeding strategies, or of multiple predators attacking each pest species, would all potentially improve the stability of biological control across habitats.

The biodiversity-functioning relationship has been the focus of a long-term research emphasis (Schlapfer & Schmid 1999; Loreau *et al.* 2001; Hooper *et al.* 2005; Díaz *et al.* 2006), and studies adopting a food-web approach are shedding light on the mechanisms underpinning this relationship and how they may be applied to entire multi-trophic communities (Montoya *et al.* 2003; Rooney & McCann 2012). This work further demonstrates that parasitism rates are enhanced by the presence of complementary trophic interactions among species (i.e. low niche overlap) rather than by diversity *per se*, and thereby demonstrates that previous findings at the pair-wise interaction level (Finke & Snyder 2008) do indeed scale up to the community level. Moreover, it shows that parasitoid redundancy provides spatial insurance effects that reduce site-to-site variability in parasitism,

which bears important consequences for landscape-scale management of crop pests (Tscharntke *et al.* 2007). By placing a stronger conceptual emphasis on networks of interacting species, a food-web approach can be very useful for scaling up mechanisms to predict community responses and changes to ecosystem functioning.

Chapter V

Discussion

Ecosystems are constantly being modified by anthropogenic activities, which result in population declines and losses of species at unprecedented rates (Pimm *et al.* 1995; Sala *et al.* 2000; Millenium Ecosystem Assessment 2005). Moreover, these human-driven environmental changes can also affect the interactions between species (Memmott *et al.* 2007; Tylianakis *et al.* 2007; Macfadyen *et al.* 2009; Gagic *et al.* 2012), causing severe indirect effects among species as well as affecting ecosystem functions. Therefore, understanding how species interdependencies are affected by environmental changes will lead to better predictions of future outcomes (McCann 2007; Bascompte 2009) as well as better conservation and management strategies (Brose 2010; Tylianakis *et al.* 2010).

The aim of this thesis was to add to knowledge of the response of biotic interactions to environmental changes. To highlight the importance of studying communities rather than species, I focused on the response of feeding interaction networks (food webs), to one of the most pervasive features of habitat fragmentation, habitat edges, which has been largely overlooked in the food-web literature (but see Macfadyen & Muller 2013). I found that, despite the fact that the composition of species and interactions of native and managed habitats merge at their interface, the way in which those interactions are structured at habitat edges could not be predicted from their adjacent counterparts (Chapter II). This reflects how environmental changes can have effects beyond species composition *per se*, and calls for the incorporation of interaction-network structure into studies evaluating such changes. I also found that not only did species composition across trophic levels change across a habitat edge gradient, but also that phylogenetic diversity was affected (Chapter III). Even more, the

signal of coevolution also changed between native vs. managed habitats (Chapter III), reflecting selection of particular coevolved interactions in anthropogenic modified habitats, which may potentially interfere with natural evolutionary processes. Despite these differences, parasitism rates did not change across native vs. managed habitats, nor between edge vs. interior locations within habitats (Chapter III). Finally, by using structural characteristics of food webs, I determined the mechanisms driving consumption rates and their stability (Chapter IV), thereby linking food-web structure to ecosystem functioning. I found that complementarity and redundancy in resource-use among predators increased attack rates and their spatial stability respectively.

5.1 Food webs at the landscape level

Fragmentation is a complex process by which habitats are partitioned into smaller patches, altering the structure and composition of the landscape mosaic (Wilcove *et al.* 1986; Fahrig 2003). The study of food webs in a fragmentation context has so far looked primarily at differences across habitat types (Tylianakis *et al.* 2007; Macfadyen *et al.* 2009), isolation of patches of a given habitat (Kaartinen & Roslin 2011), restored vs. unrestored habitats (Albrecht *et al.* 2007; Henson *et al.* 2009), and fragment size (Valladares *et al.* 2012). All these studies were pioneers in looking at the effects of contemporary environmental changes on the reticulate web of feeding interactions within communities and their structure. However, different habitat types or patches of a single habitat type are not isolated in a hostile matrix, but they rather form part of a mosaic of different juxtaposed habitat types that interact with one another (Ricketts 2001; Blitzer *et al.* 2012; Tscharntke *et al.* 2012b). These boundaries among habitat types have been a key area of study by ecologists for decades (Hansen *et al.* 1988). However, they have been widely studied only for pair-wise interactions

(e.g. Fagan *et al.* 1999; Ries *et al.* 2004; Ewers *et al.* 2013) and from a community composition perspective (e.g. Yahner 1988; Ewers & Didham 2008; Gieselman *et al.* 2013), yet edges have been overlooked in the community-level interaction-network literature.

Because edges represent a connection among different habitat types at the landscape level, I studied in Chapter II how species interactions assemble at habitat edges with respect to the food webs of the adjoining habitats. I found that, even though composition at habitat edges can be predicted from the adjacent areas, the structure of the resulting food web cannot. This reflects how land-use change and fragmentation not only affect communities and the structure of their interactions in the altered habitats (Albrecht *et al.* 2007; Tylianakis *et al.* 2007; Macfadyen *et al.* 2009), or smaller fragments (Valladares *et al.* 2012), but also all over the edges between different habitat types. It is therefore important to account for these effects when designing conservation areas, particularly due to the potential extended effects that habitat edges can have towards interior habitats (Ewers & Didham 2008). Expansion of this work should focus on determining whether edges between habitat types of contrasting vegetation structure, i.e. 'hard edges' (Stamps *et al.* 1987), also affect the way in which species interactions assemble, as found in the 'soft edges' of this study. Because soft versus hard edges can affect dispersal of organisms in different manners (Stamps *et al.* 1987), dispersal could potentially be more restricted in 'hard edges', due to changes in habitat structure, and this may generate edge webs that resemble the '*non-stick*' hypothesis in Chapter II.

Ecologists are increasingly recognising the importance of studying food webs at the landscape level (Polis *et al.* 1997; Polis *et al.* 2004; Rooney *et al.* 2008), and food-web complexity has recently been shown to respond to landscape complexity (Gagic *et al.* 2011; Rand *et al.* 2012; Fabian *et al.* 2013). As moves are made to model such landscape-scale food webs, the results in Chapter II demonstrate that landscapes cannot be treated as a simple

collection of different habitat patches. Rather, the web at the edge of each patch will be a function of the species and interactions available in the adjacent habitats, along with some selection of these due to edge effects, and this will therefore generate within-patch heterogeneity in food-web structure.

5.1.1 Caution in relating communities to structure

Species composition and food-web structure are not always tied together. In previous studies, it has been shown that food-web structure can differ across habitats beyond simple changes in species composition (Tylianakis *et al.* 2007), and that species composition can vary across communities that do not differ in their interaction-network structure (Kaartinen & Roslin 2011). In addition to this, Chapter II demonstrated that habitat edges can affect the structure of food webs in a way that is not a direct consequence of the community composition.

Therefore, it is necessary to bear in mind that interactions and food-web structure *per se* can be susceptible to environmental changes, independent of changes in community composition. These findings call for caution in studies (e.g. Romanuk *et al.* 2006; Coll *et al.* 2008; Piechnik *et al.* 2008) that attempt to reconstruct structural patterns of local food webs by knowing the species composition of each community and their potential interactions based on the literature, as not all potential interactions may be realised at a given location (Laliberte & Tylianakis 2010).

Nevertheless, reconstruction of food webs in this way becomes less necessary as the field and laboratory effort needed for food-web studies declines with the increasing availability and decreasing cost of new techniques (e.g. molecular tools) (Poole *et al.* 2012).

This will hopefully allow for an easier detection of interactions as well as the incorporation of even more trophic levels and guilds, so that a better estimation of the entire ecosystem can be achieved (Kaartinen *et al.* 2010).

5.2 Incorporating evolution for understanding contemporary ecosystems

5.2.1 Phylogenetic diversity and niche partitioning

Species and community patterns, such as their distributions (Ricklefs 1987), can be influenced not only by ecological phenomena, but also by evolutionary processes. Therefore, merging the fields of ecology and evolution has been recently promoted (Webb *et al.* 2002; Mouquet *et al.* 2012) as an important way of better understanding ecosystems and their functioning (Srivastava *et al.* 2012). Phylogenetic diversity of communities (information on the evolutionary history of their species) has been suggested to relate to ecosystem functions (Cadotte *et al.* 2009; Gravel *et al.* 2012; Srivastava *et al.* 2012), because it explains some of the functionally-important aspects of biodiversity, such as niche breadth (Wiens *et al.* 2010) and species interactions (Rezende *et al.* 2007; Bersier & Kehrli 2008; Gómez *et al.* 2010). However, even though it may inform about ecosystem functions, it does not explain the mechanisms behind those functions. As shown in this thesis, more-closely-related parasitoid species tended to consume closely-related herbivore species (Chapter III), and hence phylogenetic diversity of parasitoid communities could be informative of the subset of the herbivore community that is consumed. However, phylogenetic diversity did not affect parasitism rates as expected (Chapter III), and even though phylogenetic diversity may inform about predator niche breadths, it did not seem to be an efficient measure of resource

use complementarity, the mechanism underlying parasitism rates (Chapter IV). For example, if there is a generalist parasitoid within a group of related parasitoids that attack related hosts, there might still be detectable congruence among host-parasitoid phylogenies, even though the degree of complementarity would not be very well represented. Nevertheless, the possibility remains that phylogenies estimated by taxonomy (as used in my thesis) underestimate evolutionary distances among species, such that the phylogenetic diversity of the parasitoid communities may have been underestimated and could have reduced the detectability of differences between predator niches.

5.2.2 Signals of coevolution

The combination of phylogenetic data with species interaction patterns can provide information about the coevolutionary patterns among species (Brooks 1979; Klassen 1992; Legendre *et al.* 2002). Determining coevolutionary patterns, and how are they affected by environmental changes, can help us to determine potential cascading effects across trophic levels as well as coextinction among interacting species (Legendre *et al.* 2002; Ives & Godfray 2006; Rezende *et al.* 2007; Thompson 2009).

Whereas the early work on coevolution focused on local populations (Thompson 1999), it has become clear that, to understand how coevolution organizes diversity across complex landscapes, coevolving interactions need to be investigated across species distribution ranges (Lavandero & Tylianakis 2013; Thompson 2009). Therefore, in Chapter III, I studied how the coevolutionary signal among consumer-resource trophic levels is affected by anthropogenic habitat modification. I found that the coevolutionary signal between parasitoids and their hosts was stronger in the managed habitat compared with the native habitat, suggesting that land-use change may be forcing consumer species to feed on

those hosts for which they are better adapted, or by driving extinct those species that feed on phylogenetically-diverse prey. It is possible that monoculture plantations could be imposing a stress on parasitoids, reducing their ability to deal with a broader range of hosts (a mechanism suggested to occur with climate warming; Lavandero & Tylianakis 2013). Another possibility is that the diminished structural complexity of monoculture plantations increases the hunting efficiency of parasitoids (Brose *et al.* 2005), and hence parasitoids could choose to forage on those hosts that are more energetically rewarding, which could potentially be those with which they have coevolved.

This pattern of higher congruence among interacting predator and prey phylogenies has been also observed for host-parasitoid systems that experience higher temperatures (Lavandero & Tylianakis 2013). Combined, these results may suggest that global environmental changes may reduce predator niche breadth plasticity, which could reduce food-web resilience and with it the effectiveness of biological control programmes (Lavandero & Tylianakis 2013).

5.3 The importance of ecosystem stability

The maintenance of ecosystem functions through time and space is important for human well-being (Díaz *et al.* 2006), and in an effort to preserve them, much research has focused on the effect of diversity on the stability of ecosystem functions. According to the 'insurance hypothesis', diverse communities are better than individual species at maintaining consistent levels of an ecosystem function across a range of conditions, such that high diversity may buffer against the effects of environmental variation (Yachi & Loreau 1999). In Chapter IV, I found that the mechanism behind this hypothesis, spatial redundancy in host use by parasitoids, exerted the predicted effect on parasitism rates. This spatial insurance

effect (Loreau *et al.* 2003), reinforces the idea that communities, although usually studied as independent entities, are embedded in a landscape mosaic with other communities that interact through dispersal of organisms (Wilson 1992; Mouquet & Loreau 2003; McCann *et al.* 2005; Kremen *et al.* 2007). As I showed in Chapter II, herbivores and parasitoids are moving across habitats, connecting the different habitats and food webs therein. Therefore, acquiring a more holistic landscape perspective will allow us to understand how ecosystem functions are affected and/or benefit not only from characteristics of the local habitat, but also from surrounding different habitat types.

5.4 **Informing conservation strategies**

Whether conservation land should be separated from production areas (land sparing) or integrated within the same area (land sharing), has been widely debated (Wagooner 1996; Green *et al.* 2005; Balmford *et al.* 2012). Proponents of land sparing have generally assumed that by increasing land intensification, higher production would be obtained per unit area, and hence less area should be required for obtaining food and goods, leading to the preservation of larger natural areas (Green *et al.* 2005; Fischer *et al.* 2008; Phalan *et al.* 2011). However, this perspective overlooks the fact that land-use intensification does not always spare land for nature (Ewers *et al.* 2009; Godfray 2011) and that intensification can also disturb ecosystem functions such as pest control and pollination, which could end up affecting the long-term sustainability of production areas (Tscharntke *et al.* 2012a). Moreover, the results of Chapter II revealed that increased intensification of production habitats may alter the conservation value of adjacent natural habitats via edge effects, which suggests a need for edge effects to be incorporated into the debate. For example, in a land sparing context, conservation areas should be delimited taking into account edge effects, such

that they have a large enough size to preserve more pristine interior-habitat food webs. Hence, to give a more precise idea of the preservation area required to maintain natural communities without affecting their food-web structure, future work should look at how far these effects spread towards habitat interiors, in particular towards interior conservation areas.

In a similar vein, preserving core native habitat may also contribute to the conservation of genetic variability concentrated in these habitats. For example, Chapter III showed that, even though there was no difference in herbivore species richness across habitats, the native interior habitats harboured a larger number of herbivore clades compared with habitat edges and plantation forests. Therefore, by fragmenting and/or transforming native habitats into other habitat types, we are reducing the reservoir areas for genetic variation, and hence homogenizing herbivore communities. Biotic homogenization of species composition due to anthropogenic habitat modification has been also shown to occur in plant communities (Rooney *et al.* 2004), plant-pollinator systems (Dormann *et al.* 2007), and in host-parasitoid communities and their interactions (Laliberte & Tylianakis 2010), although these studies only accounted for taxonomic homogenization, and not phylogenetic relationships. Biotic homogenization is particularly relevant for resilience, because it narrows the available range of species responses (Olden *et al.* 2004), thereby reducing the possible responses of entire communities to further changes in the environment. Hence, by preserving phylogenetic variability, such as I found for herbivore communities in native interior forests, the probability of those communities and their interacting partners persisting increases.

Even though the importance of including evolutionary information into conservation practice has been widely discussed (Erwin 1991; Vane-Wright *et al.* 1991; Bininda-Emonds *et al.* 2000; Winter *et al.* 2013), little research has measured the effects of environmental changes on the phylogenetic composition of communities. Given the ubiquity of

environmental changes, plenty of opportunities for research exist in this area. Even when no fully-resolved phylogenies are available, alternative methods for estimating phylogenetic relationships (Srivastava *et al.* 2012), such as those used in this thesis (Poulin & Mouillot 2003; Cagnolo *et al.* 2011), can be employed. Despite the risk that this method may underestimate evolutionary differences compared with real phylogenies (Weiblen *et al.* 2006), it nevertheless provides a proxy for phylogenetic responses to environmental changes, allowing research to continue without being delayed by the absence of robust molecular phylogenies.

5.5 **Informing biological control strategies**

Biological control requires the combination of knowledge on community composition, dynamics and species interactions in both natural and managed areas. Research has found that natural areas close to managed areas provide a reservoir for natural enemies (Fabian *et al.* 2013), and also increase the complexity of landscapes, which can enhance biological control (Landis & Haas 1992; Marino & Landis 1996; Thies & Tscharntke 1999). However, habitats within a landscape are not independent entities, but rather share borders among them, and movement of agents across the border from natural to production areas has been widely studied in the biological control literature (Landis *et al.* 2000), even though movement in the opposite direction has received considerably less attention (Rand *et al.* 2006; but see Macfadyen & Muller 2013).

Habitat edges have been often observed to increase the abundance of natural enemies, as well as to support higher attack rates compared with habitat interiors (McGeoch & Gaston 2000; Valladares *et al.* 2006). This has been usually attributed to adjacent habitats providing alternative resources, oviposition and overwintering sites (Corbett & Rosenheim 1996;

Landis *et al.* 2000; Tylianakis *et al.* 2004), which favour particularly predators that are generalist in the habitats and/or resources they use. Therefore, anthropogenic systems can benefit from having different adjoining areas that provide important subsidies to generalist predators (Landis *et al.* 2000; Symondson *et al.* 2002). Moreover, because generalist predators are easily subsidised (Rand *et al.* 2006), they are particularly effective at controlling prey (Symondson *et al.* 2002), due to their dynamics being uncoupled from those of each specific prey species, so they can make particularly effective control agents.

In Chapter II, I found that trophic generalists were more abundant at habitat edges, compared with the null expectations derived from blending of the interior habitats. This generalist consumption behaviour may allow them to respond to changes in prey densities, i.e. switching from a less abundant to a more abundant prey species. Providing that this response is rapid, this coupling of different energy channels could confer stability to the food web (Rooney *et al.* 2006). Hence, from a biological control perspective, having more generalist species could alleviate potential pest outbreaks as generalist predators switch to the more abundant herbivore species present. Therefore, having larger edge-to-interior ratios could be beneficial for crops and plantations, particularly monocultures. However, this should not be achieved by fragmenting pristine habitats, because these natural areas could harbour biological control agents that may have not yet colonized the production area, but which could be useful in the future.

Even though I did not find changes in parasitoid attack rates across habitats (Chapter III), my findings in Chapter IV suggest that to increase parasitism rates over the entire herbivore community, and hence reduce herbivore damage on the crop/plantation (Cardinale *et al.* 2003), the maintenance of multiple enemy species with complementary (non-overlapping) resource-use is highly desirable. Therefore, if we were to introduce new agents, it would be important that they attack hosts that are attacked by no or few existing natural

enemies. This would bring the benefit of increasing pest control without displacing any existing enemies. Conversely, my results suggest that the introduction of a new specialist control agent to a system where several such agents already exist is likely to bring marginal if any control benefits.

Although in this study all the parasitoids attacked the same life stage of their host (larvae), control could be improved by providing different predators that complement each other in the host life stage they attack (Wilby & Thomas 2002; De Roos *et al.* 2008; Ramirez & Snyder 2009; Tylianakis & Romo 2010). This could be particularly useful for tackling single-species pest outbreaks. The adoption of a food-web approach not only allows for a better delimitation of host-range among predators, which can be useful for the before mentioned management strategies (Landis *et al.* 2000), but also for reducing non-desirable non-target effects.

5.6 **Conclusions**

The importance of environmental change effects on ecological interactions as key components of ecosystems has been suggested for decades (Janzen 1970; Janzen *et al.* 1976; Harrington *et al.* 1999; McCann 2007; Bascompte 2009), with the extinction of ecological interactions potentially being the most widespread form of extinction (Janzen 1974). These are the reasons why biotic interactions need to be incorporated into future predictions of community responses to perturbations, which will in turn allow us to better forecast the outcome of environmental changes.

I have shown that by adopting a food-web approach, trophic interaction structure can predict functioning, and that in combination with phylogeny it can provide insights into

coevolutionary processes and how they are affected by land-use change. Moreover, I showed that habitat edges affect the assemblage of interactions such that interactions from adjacent habitats combine in an unexpected manner. With environmental changes continually and increasingly modifying ecosystems, it has become imperative to make use of new tools that, rather than focusing on particular species, allow for a more holistic view of communities and ecosystems.

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Appendix 2

Appendix 2.1: Supplementary figures

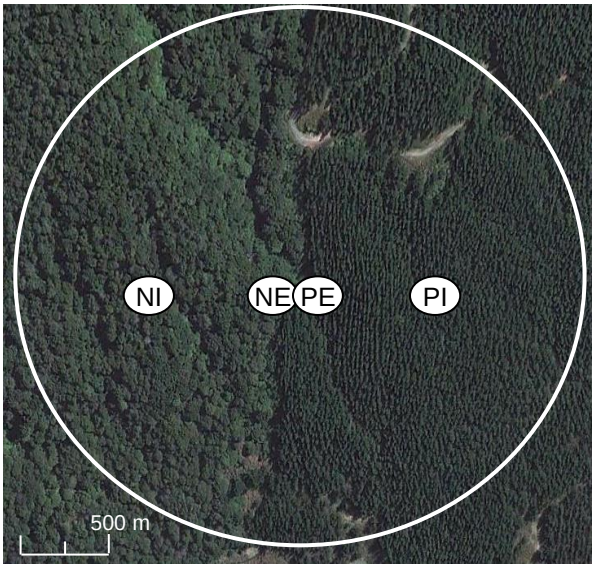

Figure S2.1: Sampling design of one site composed by native interior forest (NI), native side of the edge (NE), plantation side of the edge (PE) and plantation interior forest (PI). In total 8 sites were sampled in the Nelson/Marlborough region in New Zealand.

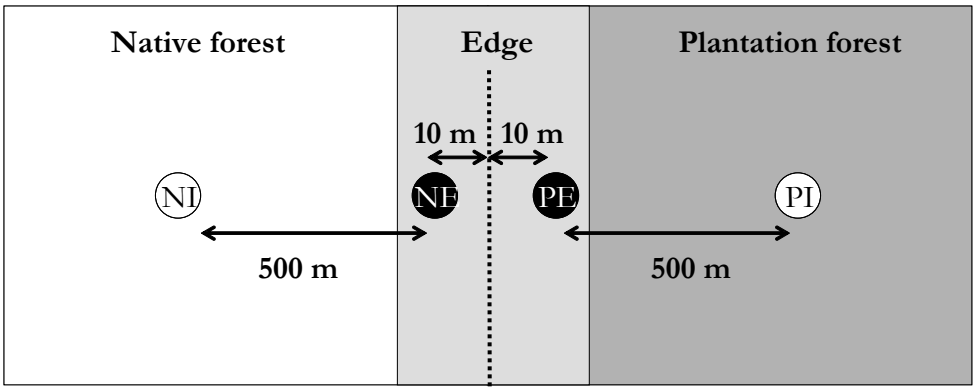

Figure S2.2: Schematic diagram of each sampling site. Each site (of eight sites in total) comprised a native forest adjacent to a pine forest. The dotted line indicates the centre of the edge zone, defined as the last row of pine trees in the plantation forest. In each forest type there were two locations (edge vs. interior), represented by black and white circles respectively. Each forest type within a site was treated as a plot, and each subplot was a specific location (edge vs. interior) within the plot. Therefore, at each site four subplots were sampled: NI) native interior forest, NE) native edge, PE) plantation edge, and PI) plantation interior forest. In total, 32 subplots were sampled across the eight sites, and a quantitative parasitoid-host food web was constructed for each subplot. For testing of the '*blended'* vs. '*hyper'* web hypotheses, the two interior webs (NI + PI) were combined into a single interior metaweb, and the two edge webs (NE + PE) into a single empirical edge web.

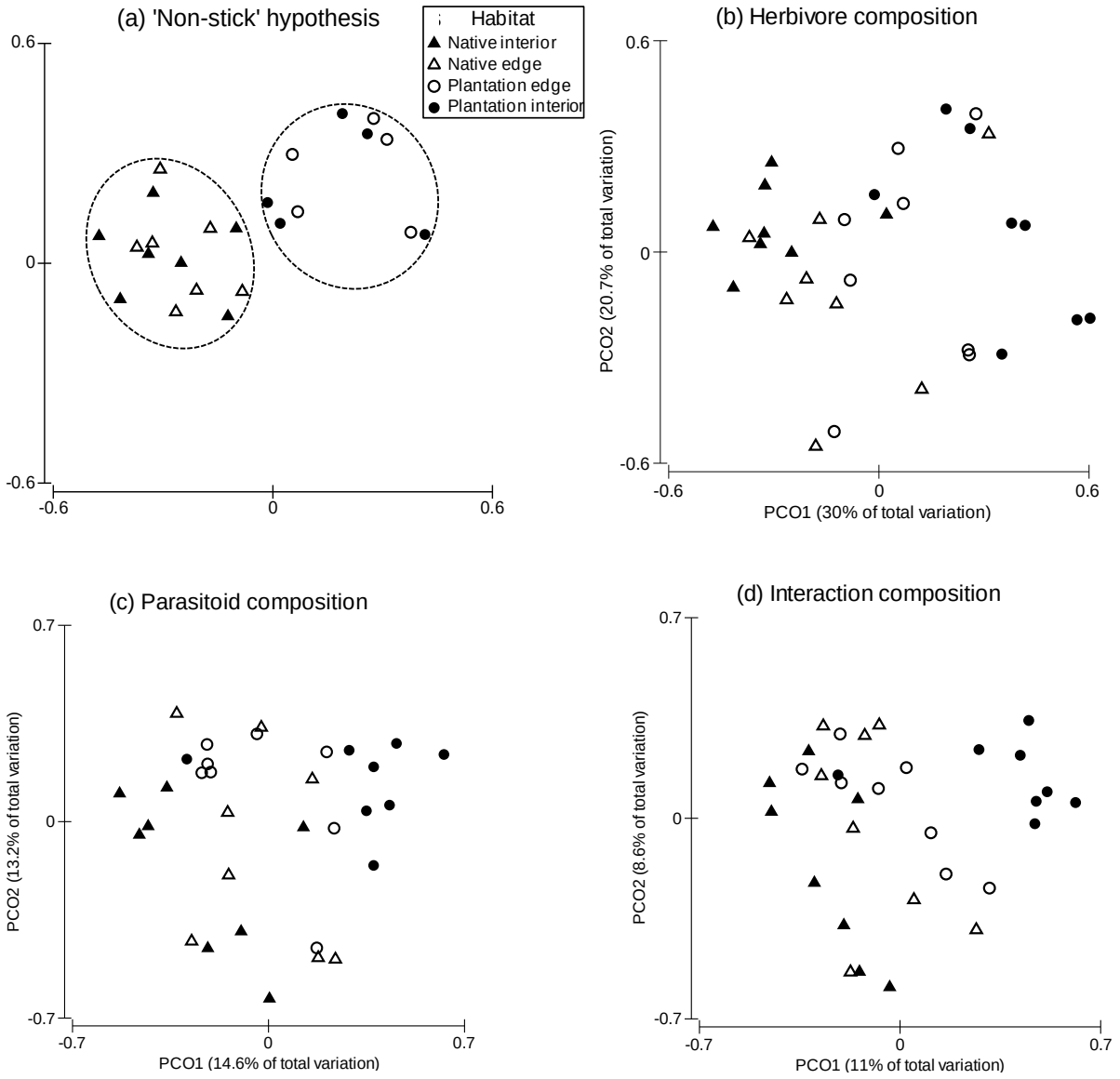

Figure S2.3: Principal Coordinate analyses (PCO) showing (a) diagram of the expected composition based on a true *'non-stick'* hypothesis, where the edge marks a division between community compositions of different forest types, and variation in the observed community composition of (b) herbivore, (c) parasitoid, and (d) herbivore-parasitoid interactions, based on a Hellinger distance metric.

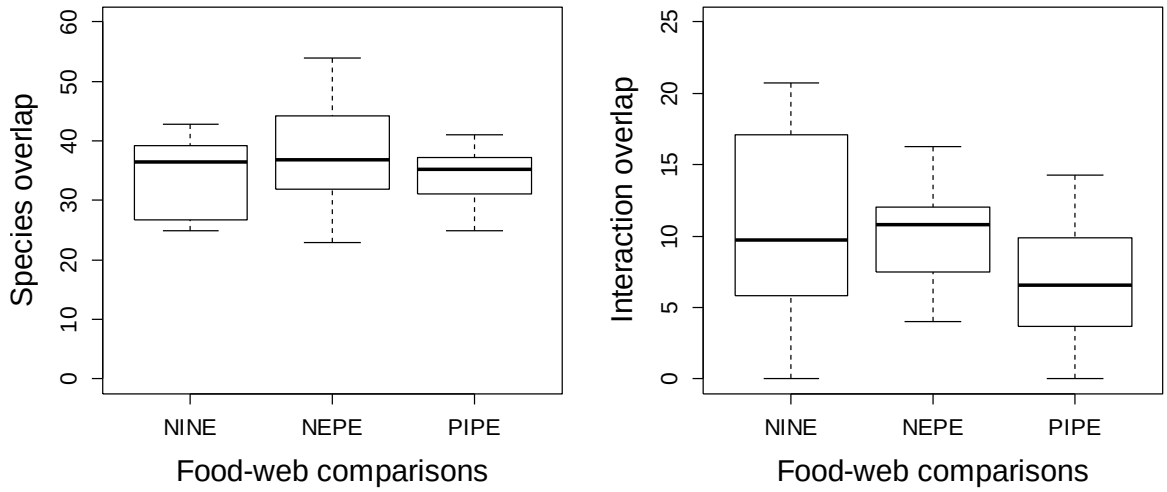

Figure S2.4: Species and interaction overlap (measured with Jaccard similarity index) among interior and edge webs within native forest (NINE), between adjacent edges belonging to different forest types (NEPE) and among interior and edge webs within plantation forest (PIPE). There were no significant differences in the amount of overlap for each comparison, suggesting a lack of support for the '*non-stick'* hypothesis.

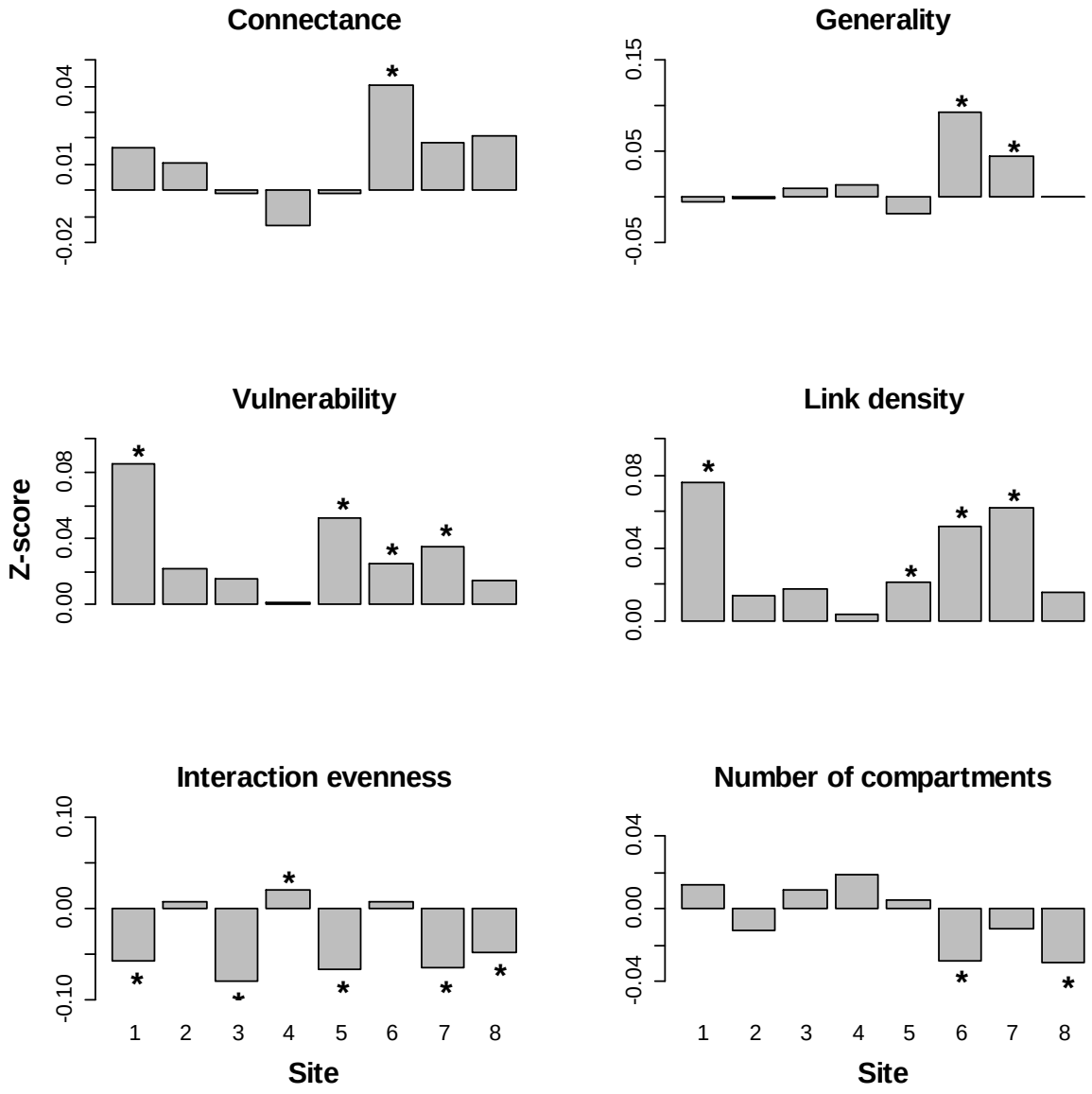

Figure S2.5: Standardised differences (Z scores) between observed vs. expected quantitative food-web metrics under the homogeneous null-probability model across the 8 sites. * = empirical value significantly different from the null expectation ($\alpha = 0.05$).

Appendix 2.2: Supplementary tables

Table S2.1: List of A) plant, B) herbivore and C) parasitoid species sampled. Species are listed by family alphabetically. Families are indicated in bold and alien species with *. Voucher specimens of plants have been deposited at the University of Canterbury Herbarium (CANU), Ichneumonidae and Tachinidae parasitoids at the New Zealand Arthropod Collection (NZAC) in Auckland, and Braconidae, Campopleginae, Chalcididae and Eulophinae parasitoids at the Te Papa Museum Entomology Collection in Wellington, NZ.

A) Plant species
Araliaceae
Pseudopanax anomalus (Hook.) K.Koch, 1859
Pseudopanax arboreus (Murray) Philipson, 1965
Pseudopanax K.Koch, 1859 sp.
Schefflera digitata J.R.Forst. & G.Forst., 1776
Aspleniaceae
Asplenium oblongifolium Colenso, 1845
Asplenium polyodon G.Forst., 1786
Berberidaceae
* *Berberis* L., 1753 sp.
Blechnaceae
Blechnum L., 1753 sp.
Blechnum discolour (G.Forst.) Keyserl., 1873
Blechnum minus (R.Br.) Ettingsh., 1864
Caprifoliaceae
* *Leycesteria Formosa* Wall., 1824
Compositae
Brachyglottis repanda J.R.Forst. & G.Forst., 1775
Helichrysum lanceolatum (Buchanan) Kirk, 1899
Olearia avicenniifolia (Raoul) Hook.f., 1864
Olearia rani (A.Cunn.) Druce, 1917
Senecio L., 1753 sp.
Coriaceae
Coriaria arborea Linds., 1868
Cunoniaceae
Weinmannia racemosa L.f., 1781
Cyatheaceae
Cyathea colensoi (Hook.f.) Domin, 1929
Cyathea dealbata (G.Forst.) Sw., 1801
Cyathea medullaris (G.Forst.) Sw., 1801
Cyathea smithii Hook.f., 1854
Dennstaedtiaceae
Histiopteris incisa (Thunb.) J.Sm., 1875
Pteridium aquilinum var esculentum (G.Forst.) Kuhn, 1882
Dicksoniaceae
Dicksonia L'Hér., 1789 sp.
Dryopteridaceae
Polystichum vestitum (G.Forst.) C.Presl, 1836

Elaeocarpaceae

Aristotelia serrata (J.R.Forst & G.Forst) W.R.B.Oliv., 1921

Elaeocarpus dentatus (J.R.Forst. & G.Forst.) Vahl, 1794

Elaeocarpus hookerianus Raoul, 1846

Ericaceae

* *Erica lusitanica* Rudolphi,

Gaultheria antipoda G.Forst., 1786

Leptecophylla juniperina (J.R.Forst. & G.Forst.) C.M.Weiller, 1999

Leucopogon fasciculatus (G.Forst.) A.Rich., 1832

Fabaceae

* *Chamaecytisus palmensis* (H.Christ) F.A.Bisby & K.W.Nicholls, 1977

Gramineae

Cortaderia richardii (Endl.) Zotov., 1963

Griselineaceae

Griselinia littoralis Raoul, 1846

Griselinia lucida G.Forst., 1786

Hemerocallidaceae

Dianella nigra Colenso, 1883

Phormium tenax J.R.Forst. & G.Forst., 1776

Lauraceae

Beilschmiedia tawa (A.Cunn.) Benth. & Hook.f. ex Kirk, 1889

Leguminosae

* *Ulex europaeus* L.

Lycopodiaceae

Lycopodium volubile G.Forst., 1786

Marattiaceae

Marattia salicina Sm., 1812

Monimiaceae

Hedycarya arborea J.R.Forst. & G.Forst., 1776

Myrtaceae

Kunzea ericoides (A.Rich.) Joy Thomps., 1983

Leptospermum scoparium J.R.Forst. & G.Forst., 1776

Lophomyrtus obcordata (Raoul) Burret, 1941

Lophomyrtus bullata (Sol. Ex A.Cunn.) Burret, 1941

Metrosideros diffusa (G.Forst.) Sm., 1797

Metrosideros fulgens Sol. ex Gaertn., 1788

Neomyrtus pedunculata (Hook.f.) Allan, 1961

Nothofagaceae

Nothofagus fusca (Hook.f.) Oerst., 1873

Nothofagus menziesii (Hook.f.) Oerst., 1873

Nothofagus solandri var solandri (Hook.f.) Oerst.

Nothofagus truncata (Colenso) Cockayne

Oleaceae

Nestegis montana (Hook.f.) L.A.S.Johnson, 1958

Onagraceae

* *Fuchsia excorticata* (J.R.Forst. & G.Forst.) L.f., 1781

Osmundaceae

Leptopteris hymenophylloides (A.Rich.) C.Presl, 1846

Paracryphiaceae
Quintinia serrata A.Cunn., 1839
Passifloraceae
Passiflora tetrandra Banks ex DC., 1828
Pennantiaceae
Pennantia corymbosa J.R.Forst. & G.Forst., 1776
Pinaceae
* *Pinus radiata* D.Don
* *Pinus sylvestris* L.
* *Pseudotsuga menziesii* (Mirb.) Franco
Pittosporaceae
Pittosporum eugenioides A.Cunn., 1840
Pittosporum rigidum Hook.f., 1852
Pittosporum Banks & Sol. ex Gaertn., 1788 sp.
Plantaginaceae
* *Digitalis purpurea* L.
Hebe Juss., 1789 sp.
Podocarpaceae
Dacrydium cupressinum Lamb., 1803
Podocarpus hallii Kirk, 1889
Podocarpus L'Her. ex Pers., 1807 sp.
Podocarpus totara G.Benn. ex D.Don, 1832
Prumnopitys ferruginea (D.Don) de Laub., 1978
Prumnopitys taxifolia (D.Don) de Laub., 1978
Polypodiaceae
Microsorum pustulatum (G.Forst.) Copel.,1947
Microsorum scandens (G.Forst.) Tindale, 1960
Primulaceae
Myrsine australis (A.Rich.) Allan, 1947
Ripogonaceae
Ripogonum scandens J.R.Forst. & G.Forst., 1776
Rosaceae
Rubus cissoides A.Cunn., 1839
* *Rubus fruticosus* L.
Roussaceae
Carpodetus serratus J.R.Forst. & G. Forst., 1776
Coprosma aff intertexta G. Simpson, 1945
Coprosma areolata Cheeseman, 1885
Coprosma colensoi Hook.f., 1864
Coprosma foetidissima J.R.Forst. & G.Forst., 1776
Coprosma grandifolia Hook.f., 1852
Coprosma linariifolia Hook.f., 1864
Coprosma lucida J.R.Forst. & G.Forst., 1776
Coprosma microcarpa Hook.f., 1853
Coprosma propinqua A.Cunn., 1839
Coprosma rhamnoides A.Cunn., 1839
Coprosma robusta Raoul, 1844
Coprosma robusta x *Coprosma propinqua* Raoul

Coprosma rotundifolia A.Cunn., 1839
Sapindaceae
Alectryon excelsus Gaertn., 1788
Violaceae
Melicytus ramiflorus J.R.Forst. & G.Forst., 1776
Winteraceae
Pseudowintera axillaris (J.R.Forst. & G.Forst.) Dandy, 1933
Pseudowintera colorata (Raoul) Dandy, 1933

B) Herbivore species
Arctiidae
Nyctemera annulata (Boisduval, 1832)
Carposinidae
Heterocrossa gonosemana Meyrick, 1882
Heterocrossa Meyrick, 1882 sp. 'indet A'
Paramorpha marginata (Philpott, 1931)
Crambidae
Deana hybreasalis (Walker, 1859)
Musotima nitidalis (Walker, 1866)
Erebidae
Rhapsa scotosialis Walker, 1866
Gelechiidae
Thiotricha Meyrick, 1886 sp.
Thiotricha lindsayi Philpott, 1927
Geometridae
Austrocidaria Dugdale, 1971 sp.
Chalastra pellurgata Walker, 1862
Chloroclystis Hubner, [1825] sp.
Cleora scriptaria (Walker, 1860)
Declana feredayi Butler, 1877
Declana floccosa Walker, 1858
Declana hermione Hudson, 1898
Declana junctilinea (Walker, 1865)
Declana leptomera (Walker, 1858)
Declana niveata Butler, 1879
Elvia glaucata Walker, 1862
Gellonia Meyrick, 1884 sp.
Helastia Guenée, 1868 sp.
Hydriomena deltoidata (Walker, 1862)
Ischalis gallaria (Walker, 1860)
Ischalis variabilis (Warren, 1895)
Pasiphila sandycias (Meyrick, 1905)
Poecilasthena Warren, 1894 sp.
Pseudocoremia ampla (Hudsonb, 1923)
Pseudocoremia fascialata (Philpott, 1903)
Pseudocoremia fenerata (Felder & Rogenhofer, 1875)
Pseudocoremia fluminea (Philpott, 1926)

Pseudocoremia leucelaea (Meyrick, 1909)
Pseudocoremia lupinata (Felder & Rogenhofer, 1875)
Pseudocoremia productata (Walker, 1862)
Pseudocoremia Butler, 1877 sp.
Sarisa muriferata (Walker, 1863)
Sestra Walker, 1862 sp.
Tatosoma lestevata (Walker, 1862)
Tatosoma tipulata (Walker, 1862)
Xyridacma alectoraria (Walker, 1860)
Xyridacma ustaria (Walker, 1863)
Gracillariidae
Caloptilia linearis (Butler, 1877)
Caloptilia selenitis (Meyrick, 1909)
Noctuidae
Austramathes purpurea (Butler, 1879)
Andesia pessota (Meyrick, 1887)
Chrysodeixis eriosoma (Doubleday, 1843)
Feredayia graminosa (Walker, 1857)
Graphania insignis (Walker, 1865)
Graphania mutans (Walker, 1857)
Graphania plena (Walker, 1865)
Graphania ustistriga (Walker, 1857)
Meterana dotata (Walker, 1857)
Meterana pascoi (Howes, 1912)
Meterana vitiosa (Butler, 1877)
Physetica prionistis Meyrick, 1887
Physetica sequens Howes, 1912
Nolidae
Celama parvitis Howes, 1917
Oecophoridae
* *Eutorna phaulocosma* Meyrick, 1906
Gymnobathra Meyrick, 1883 sp.
Nymphostola galactina (Felder & Rogenhofer, 1875)
Phaeosaces Meyrick, 1886 sp.
Proteodes profunda Meyrick, 1905
Plutellidae
Orthenches Meyrick, 1886 sp.
Psychidae
Grypotheca pertinax Dugdale, 1987
Liothula omnivora Fereday, 1878
Psychidae sp.
Stathmopodidae
Stathmopoda Herrich-Schaffer, 1853 sp. 'chocolate'
Tineidae
Erechthias externella (Walker, 1864)
Sagephora phortegella Meyrick, 1888
Tortricidae
Apoctena Dugdale, 1990 sp.

Catamacta gavisana (Walker, 1863)
Cnephasia jactatana (Walker, 1863)
Ctenopseustis Meyrick, 1885 sp.
Dipterina imbriferana Meyrick, 1881
Ecclitica torogramma (Meyrick, 1897)
Epalxiphora axenana Meyrick, 1881
Epichorista emphanes (Meyrick, 1901)
Epichorista hemiona (Meyrick, 1882)
* *Epiphyas postvittana* (Walker, 1863)
Harmologa amplexana (Zeller, 1875)
Holocola emplasta Meyrick, 1901
Holocola parthenia Meyrick, 1888
Holocola zopherana Meyrick, 1881
Leucotenes coprosmae (Dugdale, 1988)
Planotortrix excessana (Walker, 1863)
Planotortrix notophaea (Turner, 1926)
Planotortrix octo Dugdale, 1990
Pyrgotis Meyrick, 1881 sp.
Strepsicrates Meyrick, 1881 sp.
Yponomeutidae
Kessleria copidota (Meyrick, 1889)

C) Parasitoid species
Braconidae
Aleiodes declanae van Achterberg, 2005
Aleiodes Wesmael, 1838 sp.
Choeras Mason, 1981 sp.
* *Cotesia* Cameron, 1891 sp.
Dolichogenidea Viereck, 1911 sp. 2
Dolichogenidea Viereck, 1911 ‘darklegs’ sp. 4
Dolichogenidea Viereck, 1911 ‘lightly punct’
Glyptapanteles Ashmead, 1904 ‘dark’
Glyptapanteles Ashmead, 1904 sp. 2
Glyptapanteles Ashmead, 1904 sp. 3
Glyptapanteles Ashmead, 1904 sp. 4
Glyptapanteles Ashmead, 1904 sp. 5
Glyptapanteles Ashmead, 1904 sp.6
Glyptapanteles Ashmead, 1904 sp. 8
Glyptapanteles Ashmead, 1904 sp. 9
* *Meteorus cinctellus* (Spinolla, 1808)
Meteorus cobbus Huddleston, 1986
* *Meteorus pulchricornis* (Wesmael, 1835)
Campopleginae
Diadegma Forster, 1868 ‘brown ’
Diadegma Forster, 1868 ‘gold setae’
Diadegma Forster, 1868 sp. 1
Diadegma Forster, 1868 sp. 3

Eulophidae
Sympiesis Forster, 1856 sp.
Zealachertus Boucek, 1978 sp.
Zealachertus tortriciphaga Berry, 1999
Ichneumonidae
Aucklandella Cameron, 1909 sp.
Campoletis Forster, 1868 sp. 1
Campoletis Forster, 1868 sp. 4
Campoletis Forster, 1868 sp. 5
Campoletis Forster, 1868 sp. 9
Campoplex Gravenhorst, 1829 sp. 1
Campoplex Gravenhorst, 1829 sp. 13
Campoplex Gravenhorst, 1829 sp. 2
Campoplex Gravenhorst, 1829 sp. 3
Campoplex Gravenhorst, 1829 sp. 4
Campoplex Gravenhorst, 1829 sp. 9
Carria fortipes (Cameron, 1898)
Carria Schmiedeknecht, 1924 'no areolet'
Carria Schmiedeknecht, 1924 'petiolte areolet'
Carria Schmiedeknecht, 1924 sp. 2
Carria Schmiedeknecht, 1924 sp. 3
Casinaria Holmgren, 1858 sp. 3
Genus nov Hearthead
Ophion Fabricius, 1798 sp.
Phytodietus Gravenhorst, 1829 sp.
Sciron Fitton, 1984 sp.
Tachinidae
Calcager dubium Malloch, 1938
Calcageria incidens Curran, 1927
Genotrichia minor Malloch, 1938
Genotrichia Malloch, 1938 sp.
Montanarturia dimorpha (Malloch, 1938)
Pales atrox (Hutton, 1901)
Pales casta (Hutton, 1904)
Pales clathrata (Nowicki, 1875)
Pales feredayi (Hutton, 1901)
Pales funesta (Hutton, 1901)
Pales marginata (Hutton, 1901)
Plagiomyia longipes Malloch, 1938
* *Trigonospila brevifacies* (Hardy, 1934)
Uclesiella Malloch, 1938 sp.

Table S2.2: Results of PERMANOVA analysis of Jaccard dissimilarity in A) herbivore community composition, B) parasitoid community composition and C) the composition of herbivore-parasitoid interactions across different forest types and locations (edge vs. interior). Plant composition was entered as a covariate last in the model. Bold values indicate significant results ($\alpha = 0.05$).

	Source	**df**	**SS**	**MS**	**Pseudo-F**	**P(perm)**
A) Herbivore composition	Site	7	18158.0	2594.0	1.550	**0.016**
	Forest type	1	5972.9	5972.9	3.568	**<0.001**
	Plot	7	11717.0	1673.9	1.040	0.393
	Location	1	2615.0	2615.0	1.625	0.078
	Forest type * Location	1	2899.9	2899.9	1.802	**0.039**
	Plant composition	1	2306.1	2306.1	1.433	0.148
	Residuals	13	20918.0	1609.1		
	Total	31	64587.0			
B) Parasitoid composition	Site	7	27904.0	3986.3	1.510	**0.022**
	Forest type	1	6063.4	6063.4	2.297	**0.013**
	Plot	7	18477.0	2639.6	0.956	0.611
	Location	1	3700.4	3700.4	1.341	0.190
	Forest type * Location	1	3787.1	3787.1	1.372	0.177
	Plant composition	1	2515.5	2515.5	0.911	0.538
	Residuals	13	35876.0	2759.7		
	Total	31	98324.0			
C) Interaction composition	Site	7	33477.0	4782.4	1.217	0.133
	Forest type	1	7821.2	7821.2	1.991	**0.013**
	Plot	7	27499.0	3928.5	0.963	0.640
	Location	1	4354.1	4354.1	1.067	0.397
	Forest type * Location	1	5692.9	5692.9	1.395	0.116
	Plant composition	1	3747.7	3747.7	0.918	0.583
	Residuals	13	53053.0	4081.0		
	Total	31	1.356e5			

Table S2.3: Pair-wise comparisons of herbivore, parasitoid and interaction composition between edge vs. interior locations for native forest vs. plantation forest types, with A) plant composition entered last in the model, and B) plant composition entered first in the model. Bold values indicate significant results ($\alpha = 0.05$).

	Community composition	**Dissimilarity metric**	**Native**		**Plantation**	
			t-value	**P (perm)**	**t-value**	**P (perm)**
A) Plant composition last in the model	Herbivore	Jaccard	1.598	**0.015**	0.952	0.522
		Hellinger	1.571	**0.031**	1.688	**0.024**
	Parasitoid	Jaccard	1.148	0.250	1.161	0.241
		Hellinger	1.328	0.113	1.478	**0.040**
	Interaction	Jaccard	1.026	0.426	1.183	0.200
		Hellinger	1.091	0.325	1.348	0.077
B) Plant composition first in the model	Herbivore	Jaccard	1.071	0.359	0.993	0.466
		Hellinger	1.033	0.389	1.127	0.284
	Parasitoid	Jaccard	0.824	0.718	0.910	0.603
		Hellinger	1.107	0.310	1.218	0.182
	Interaction	Jaccard	0.885	0.660	1.017	0.449
		Hellinger	0.935	0.567	1.181	0.215

Table S2.4: Results of PERMANOVA analysis of Hellinger dissimilarity in A) herbivore community composition, B) parasitoid community composition and C) the composition of herbivore-parasitoid interactions across different forest types and locations (edge vs. interior). Plant composition was entered as a covariate first in the model. Bold values indicate significant results ($\alpha = 0.05$).

	Source	**df**	**SS**	**MS**	**Pseudo-F**	**P(perm)**
A) Herbivore composition	Plant composition	1	1.952	1.952	9.715	**<0.001**
	Site	7	2.852	0.407	2.047	**0.002**
	Forest type	1	0.284	0.284	1.589	0.110
	Plot	7	1.375	0.196	1.150	0.232
	Location	1	0.357	0.357	2.091	**0.044**
	Forest type * Location	1	0.258	0.258	1.509	0.139
	Residuals	13	2.222	0.171		
	Total	31	9.301			
B) Parasitoid composition	Plant composition	1	1.636	1.636	3.114	**<0.001**
	Site	7	6.019	0.860	1.651	**0.005**
	Forest type	1	0.579	0.579	1.155	0.312
	Plot	7	3.611	0.516	1.043	0.389
	Location	1	0.893	0.893	1.806	**0.044**
	Forest type * Location	1	0.682	0.682	1.378	0.165
	Residuals	13	6.432	0.495		
	Total	31	19.853			
C) Interaction composition	Plant composition	1	1.813	1.813	2.458	**0.001**
	Site	7	6.910	0.987	1.357	**0.039**
	Forest type	1	0.782	0.782	1.042	0.442
	Plot	7	5.066	0.724	0.949	0.678
	Location	1	1.081	1.081	1.417	0.119
	Forest type * Location	1	0.932	0.932	1.223	0.247
	Residuals	13	9.913	0.762		
	Total	31	26.497			

Table S2.5: Results of PERMANOVA analysis of Jaccard dissimilarity in A) herbivore community composition, B) parasitoid community composition and C) the composition of herbivore-parasitoid interactions across different forest types and locations (edge vs. interior). Plant composition was entered as a covariate first in the model. Bold values indicate significant results ($\alpha = 0.05$).

	Source	df	SS	MS	Pseudo-F	P(perm)
A) Herbivore composition	Plant composition	1	8332.5	8332.5	4.917	**<0.001**
	Site	7	18128.0	2589.7	1.560	**0.013**
	Forest type	1	1763.1	1763.1	1.087	0.373
	Plot	7	11416.0	1630.8	0.013	0.471
	Location	1	2029.3	2029.3	1.261	0.238
	Forest type * Location	1	2001.0	2001.0	1.244	0.247
	Residuals	13	20918.0	1609.1		
	Total	31	64587.0			
B) Parasitoid composition	Plant composition	1	6703.0	6703.0	2.454	**0.003**
	Site	7	28594.0	4084.9	1.548	**0.015**
	Forest type	1	2803.8	2803.8	1.051	0.404
	Plot	7	18199.0	2599.8	0.942	0.649
	Location	1	3919.4	3919.4	1.420	0.156
	Forest type * Location	1	2228.7	2228.7	0.808	0.652
	Residuals	13	35876.0	2759.7		
	Total	31	98324.0			
C) Interaction composition	Plant composition	1	8354.9	8354.9	2.084	**0.002**
	Site	7	33831.0	4833.0	1.226	0.115
	Forest type	1	4755.8	4755.8	1.194	0.267
	Plot	7	27409.0	3915.5	0.959	0.657
	Location	1	4656.6	4656.6	1.141	0.322
	Forest type * Location	1	3585.3	3585.3	0.878	0.643
	Residuals	13	53053.0	4081.0		
	Total	31	1.356e5			

Table S2.6: Results of PERMDISP analysis of differences in compositional dispersion among groups for plants, herbivores, parasitoids and herbivore-parasitoid interactions, based on both Hellinger and Jaccard dissimilarity metrics. Grouping factors in the PERMDISP analysis were forest types (native vs. plantation), locations (edge vs. interior) and forest-location combinations (native interior, native edge, plantation edge, plantation interior). Bold values indicate significant results ($\alpha = 0.05$).

Community composition	Dissimilarity metric	Forest types		Locations		Forest-location	
		F	**P**	**F**	**P**	**F**	**P**
Plant	Jaccard	2.909	0.103	4.137	0.060	3.284	0.059
	Hellinger	73.597	**<0.001**	1.418	0.355	27.091	**<0.001**
Herbivore	Jaccard	0.363	0.567	0.217	0.660	1.429	0.325
	Hellinger	0.557	0.476	0.833	0.397	1.436	0.324
Parasitoid	Jaccard	0.549	0.480	0.142	0.713	1.001	0.463
	Hellinger	0.023	0.883	0.032	0.864	0.934	0.527
Interaction	Jaccard	8.44e-06	0.998	0.306	0.596	1.457	0.340
	Hellinger	0.005	0.945	0.039	0.858	1.687	0.287

Table S2.7: Results of Analysis of Variance (ANOVA) to test the degree of species overlap and interaction overlap between edge vs. interior locations within forest types differed from the overlap between adjacent edges (blocked by site). Overlap was measured using Hellinger and Jaccard similarity indices. Native edge vs. native interior, plantation edge vs. plantation interior, and native edge vs. plantation edge formed the three levels of the factor 'Habitat comparisons'.

Response variable	Predictor variable	df	SS	MS	F	P
Species overlap (Hellinger)	Habitat comparisons	2	0.117	0.058	1.313	0.291
	Site	1	0.030	0.030	0.668	0.423
	Residuals	20	0.888	0.044		
Species overlap (Jaccard)	Habitat comparisons	2	73.200	36.600	0.626	0.545
	Site	1	4.200	4.220	0.072	0.791
	Residuals	20	1169.700	58.490		
Interactions overlap (Hellinger)	Habitat comparisons	2	0.038	0.019	1.648	0.218
	Site	1	4e-4	4e-4	0.036	0.852
	Residuals	20	0.229	0.011		
Interactions overlap (Jaccard)	Habitat comparisons	2	71.200	35.590	1.187	0.326
	Site	1	0.400	0.430	0.014	0.906
	Residuals	20	599.600	29.980		

Table S2.8: Results of PERMANOVA analysis of Hellinger dissimilarity in A) herbivore community composition, B) parasitoid community composition and C) the composition of herbivore-parasitoid interactions between pooled habitat edges (combining native and plantation edges at each site) and pooled interior forest locations (combining native and plantation interiors at each site). Bold values indicate significant results ($\alpha = 0.05$).

	Source	**df**	**SS**	**MS**	**Pseudo-F**	**P (perm)**
A) Herbivore composition	Site	7	1.751	0.250	1.944	**<0.001**
	Location	1	0.265	0.265	2.059	0.085
	Residuals	7	0.900	0.129		
	Total	15	2.916			
B) Parasitoid composition	Site	7	4.120	0.588	1.602	**0.001**
	Location	1	0.676	0.676	1.839	0.062
	Residuals	7	2.571	0.367		
	Total	15	7.366			
C) Interaction composition	Site	7	5.868	0.838	1.272	**0.006**
	Location	1	0.963	0.963	1.462	0.150
	Residuals	7	4.612	0.659		
	Total	15	11.443			

Table S2.9: Results of PERMANOVA analysis of Jaccard dissimilarity in A) herbivore community composition, B) parasitoid community composition and C) the composition of herbivore-parasitoid interactions between pooled habitat edges (combining native and plantation edges at each site) and pooled interior forest locations (combining native and plantation interiors at each site). Bold values indicate significant results ($\alpha = 0.05$).

	Source	**df**	**SS**	**MS**	**Pseudo-F**	**P (perm)**
A) Herbivore composition	Site	7	13108.0	1872.5	1.380	**0.017**
	Location	1	2045.9	2045.9	1.508	0.166
	Residuals	7	9499.1	1357.0		
	Total	15	24653.0			
B) Parasitoid composition	Site	7	18493.0	2641.9	1.314	**0.037**
	Location	1	3431.2	3431.2	1.707	0.084
	Residuals	7	14073.0	2010.5		
	Total	15	35997.0			
C) Interaction composition	Site	7	29628.0	4232.6	1.138	0.058
	Location	1	4259.5	4259.5	1.145	0.319
	Residuals	7	26032	3718.9		
	Total	15	59920.0			

Table S2.10: Bernoulli probability that the number of empirical edge webs (out of eight) that differed significantly from null expectations could have been due to chance alone, under both homogeneous and heterogeneous null models. N = number of empirical edge webs significantly different to the null distribution (see Figures 2.4, S2.5). Values in bold indicate Bernoulli probabilities lower than α (α = 0.05).

Food-web metric	Homogeneous model		Heterogeneous model	
	N	Bernoulli p-value	N	Bernoulli p-value
Connectance	1	0.371	2	0.146
Generality	2	0.146	3	**0.036**
Vulnerability	4	**0.006**	6	**<0.001**
Link density	4	**0.006**	5	**0.001**
Interaction evenness	6	**<0.001**	4	**0.006**
Number of compartments	2	0.146	2	0.146

Appendix 2.3: Permutational multivariate analyses of variance

I conducted multivariate analyses of variance in herbivore and parasitoid species composition, as well as variance in the composition of herbivore-parasitoid interactions, using Permutational Multivariate Analyses of Variance (PERMANOVA) (Anderson *et al.* 2008). The method uses dissimilarity matrices among species assemblages (subplots), and randomizes the samples to create a distribution of the pseudo-F statistic under the null hypothesis of no difference among groups. Finally, it compares the observed pseudo-F statistic, i.e. obtained from the samples, with those from the generated distribution, and calculates the proportion of the generated pseudo-F values that are greater than or equal to the observed pseudo-F value (i.e. P-values calculated by permutation). I took an approach of using two dissimilarity measures that differ in the emphasis they give to species composition vs. relative abundance, as recommended by (Anderson *et al.* 2006). First, I generated distance matrices (dissimilarity between subplot assemblages) using Hellinger distance (Legendre & Legendre 1998), which emphasizes differences in relative abundances, excludes

joint absences and gives low weight to rare species (Legendre & Gallagher 2001). I then repeated the analyses using Jaccard dissimilarity (Legendre & Legendre 1998), one of the most commonly used distance measures in ecology, in order to asses changes in composition based only on co-occurrence (presence-absence) of species (or of pair-wise interactions).

I used a four-factor model, suggested by Marti Anderson (pers. com.), with site, forest type, plot and location (edge vs. interior) as terms, and used Type I sums of squares, with the terms entered sequentially. Forest type was tested at the whole-plot level with 1, 7 d.f., while location (edge vs. interior) and the forest–type x location interaction were tested at the subplot level with 1, 13 d.f.

Appendix 2.4: Plant composition across habitats

I tested whether plant composition changed across forest types and locations (edge vs. interior) with PERMANOVA, as explained for herbivore and parasitoid compositions in the Methods section, using both Jaccard and Hellinger dissimilarity measures. I then also made pair-wise comparisons between edge/interior locations within forest type.

Plant community composition varied significantly across forest types with both metrics emphasising presence-absence (Jaccard) as well as the combined influence of differences in relative abundances with presence-absence (Hellinger). Moreover, plant community composition differences between edge and interior locations differed across forest types (forest type * location interaction) (Table S2.11, Fig. S2.5), such that in the native forest, edge and interior locations were significantly different (Hellinger: $t = 1.609$, $P = 0.036$; Jaccard: $t = 1.185$, $P = 0.011$), whereas no differences were detected among locations in plantation forest (Hellinger: $t = 1.067$, $P = 0.366$; Jaccard: $t = 1.095$, $P = 0.323$).

Regarding homogeneity of communities, I found that plant communities were more heterogeneous in the native edge and interior forest, with increasing homogeneity towards the plantation edge and plantation interior forest (Table S2.6). This was expected, given that plantation forests were mainly a monoculture of *P. radiata*.

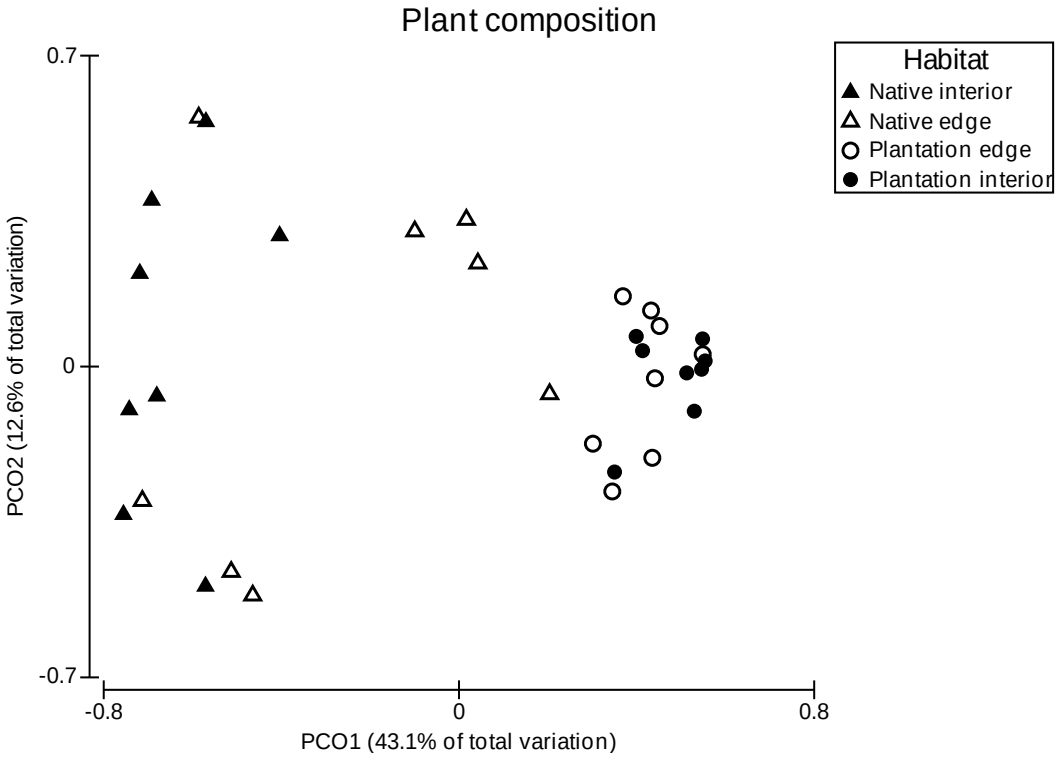

Figure S2.6: Principal Coordinate analysis (PCO) showing variation in plant community composition across forest types and locations (edge vs. interior), based on the Hellinger distance metric.

Table S2.11: Results of PERMANOVA analyses comparing Hellinger versus Jaccard measures of dissimilarity in plant community composition across different forest types and locations (edge vs. interior). Bold values indicate significant results ($\alpha = 0.05$).

Dissimilarity measure	Source	df	SS	MS	Pseudo-F	P(perm)
Hellinger	Site	7	4.957	0.708	1.819	**0.005**
	Forest type	1	6.645	6.645	17.071	**<0.001**
	Plot	7	2.725	0.389	1.602	**0.003**
	Location	1	0.512	0.512	2.107	**0.032**
	Forest type * Location	1	0.584	0.584	2.403	**0.022**
	Residuals	14	3.401	0.243		
	Total	31	18.825			
Jaccard	Site	7	33448.0	4778.3	2.013	**<0.001**
	Forest type	1	14405.0	14405.0	6.070	**<0.001**
	Plot	7	16613.0	2373.2	1.423	**0.005**
	Location	1	2820.0	2820.0	1.690	0.053
	Forest type * Location	1	819.9	4819.9	2.889	**0.002**
	Residuals	14	23356.0	1668.3		
	Total	31	95461.0			

Appendix 2.5: Food-web metrics

I calculated quantitative connectance, generality, vulnerability, link density, interaction evenness and number of compartments as food-web metrics that describe network structure. The first four metrics refer to the extent to which species interact with many other species, with connectance describing the average number of interactions per species, generality and vulnerability denoting the ratio of parasitoid to host species and vice versa, and link density defining the number of links per species. All metrics measured links weighted by their frequency of occurrence. Interaction evenness describes the similarity of interaction strengths within a web, which, with number of compartments, can give an idea of energy flow in the web.

I chose these metrics because they have been found to be good indicators of changes in network structure across habitat types (Tylianakis *et al.* 2007), and also indicators of community persistence (Thébault & Fontaine 2010), plus they have the advantage of being relatively insensitive to sampling effort compared to their qualitative counterparts (Banasek-Richter *et al.* 2004). Formulas of these metrics can be found in (Bersier *et al.* 2002) and (Tylianakis *et al.* 2007).

Appendix 2.6: Species richness of empirical edge webs and interior metawebs

In order to test if there were differences in species richness between empirical edge webs (combining adjacent edge webs from different forest types) and interior metawebs (combining interior webs from adjacent forest types) at each site, I used Generalized linear mixed-effects model in the lme4 package (Bates 2009) in R (R Core Team 2012). Number of species was entered as the response variable, location (edge vs. interior) as the predictor and site as random factor, with a Poisson error distribution.

The species richness of empirical edges webs did not differ significantly from the richness of their adjacent interior habitats combined (Z-value = -0.48, P = 0.628).

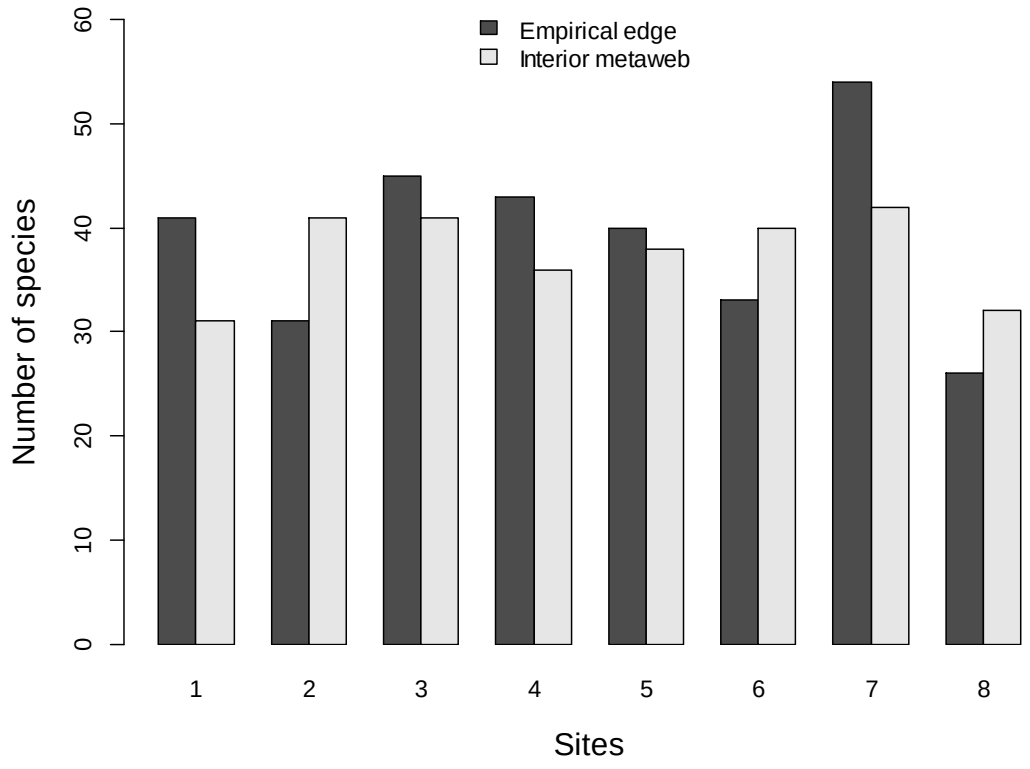

Figure S2.7: Species richness (number of species) of empirical edge webs and interior metawebs across sites. No significant differences were found between empirical edge webs and interior metawebs.

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Appendix 3

Appendix 3.1: Phylogenetic species diversity metrics

In order to quantify phylogenetic species composition of the plant, herbivore and parasitoid communities, I used three metrics that combine species relatedness information with characteristics of community composition: phylogenetic species variability (PSV), phylogenetic species richness (PSR) and phylogenetic species evenness (PSE) (Helmus *et al.* 2007). Phylogenetic species variability is calculated as:

$$PSV = \frac{ntrC - \sum C}{n(n-1)}$$

where n is the number of species in the community, C is a covariance matrix that summarizes the correlation structure of community phylogeny and trC is the sum of diagonal elements of C. It represents how distantly related are species in a community, decreasing towards zero when species are more closely related.

Phylogenetic species richness (PSR), analogous to the traditional species richness metric, is calculated by multiplying the number of species in the community (n) by the community phylogenetic variability (PSV):

$$PSR = nPSV$$

Phylogenetic species evenness (PSE) represents similarity in the abundance of the different phylogenetic groups present in a community, analogous to species evenness in abundance. It therefore incorporates not only the topology of the phylogenetic tree, but also species abundances. It is calculated as:

$$PSE = \frac{mdiag(C)'M - M'CM}{m^2 - \overline{m}_i m}$$

where m represents the total number of individuals (abundance) in the community, m_i the abundance of each species from the community (with i taking values from 1 to n), M is a vector containing values of m_i, and $\overline{m}_i$ represents a community in which species have equal abundances and are evolutionary independent (i.e. star phylogeny). Prime (‘) denotes transpose.

Appendix 3.2: Indigenous plant phylogenetic diversity

In order to determine whether differences in phylogenetic diversity of the plant communities across habitat types were due to the presence of introduced, non-indigenous species, I removed alien species from the dataset and re-calculated the phylogenetic diversity metrics (PSV, PSR, PSE). I used GLMMs (with a Gaussian error distribution) in order to determine whether there were differences across habitats in the phylogenetic diversity of plant communities, considering only indigenous plant species. I used forest type, location (edge vs. interior), and their interaction as predictor variables, and sampling plot nested within site as a random factor. I used the same model selection procedure as explained in the Methods section (main text). The response variables plant PSR and PSE were squared root transformed in order to achieve normality and homoscedasticity of variances.

The best-fitting GLMM model only retained forest type as a factor, and this only had a weak (non-significant) effect on PSV of indigenous plant species. For the other response variables, PSR and PSE, there was a significant effect of forest type, with both measures having lower values in plantation forests than in the native forests (Table S3.1, Fig. S3.2).

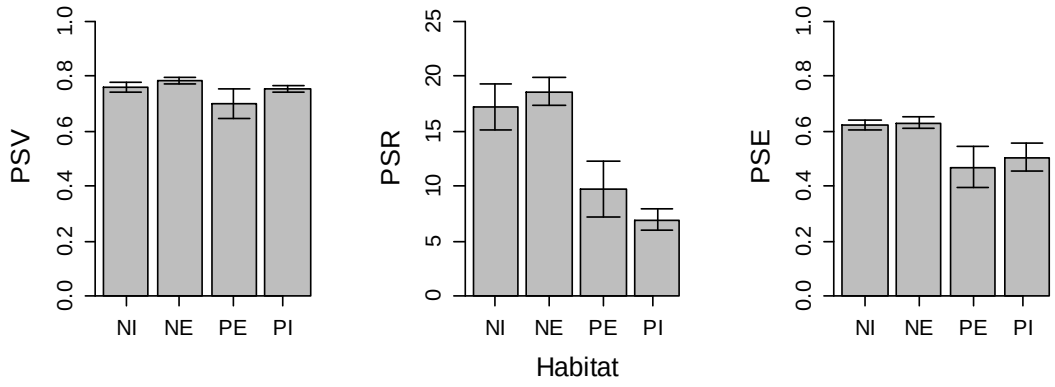

Figure S3.1: Mean (± SE) of phylogenetic species variability (PSV), phylogenetic species richness (PSR) and phylogenetic species evenness (PSE) of indigenous plant species across a habitat edge gradient. NI = native forest interior habitat, NE = native forest edge, PE = plantation forest edge, PI = plantation interior habitat.

Table S3.1: Results from GLMMs (with Gaussian error distribution) showing differences in plant phylogenetic diversity across forest types. Results are from the best-fitting model (with lowest AIC), after model selection. P-values were estimated using Markov Chain Monte Carlo procedure. PSV = phylogenetic species variability, PSR = phylogenetic species richness, PSE = phylogenetic species evenness. Bold values indicate significant results (α = 0.05). Forest P = Plantation forest.

Phylogenetic diversity metric	Fixed effects	Estimate ± SE	t-value	P_{MCMC}
Plant PSV	Intercept	0.770 ± 0.020	38.370	**<0.001**
	Forest P	-0.044 ± 0.028	-1.540	0.148
Plant PSR	Intercept	4.190 ± 0.226	18.565	**<0.001**
	Forest P	-1.443 ± 0.285	-5.071	**<0.001**
Plant PSE	Intercept	0.790 ± 0.029	26.896	**<0.001**
	Forest P	-0.111 ± 0.041	-2.691	**0.016**

Appendix 3.3: Indigenous parasitoid phylogenetic diversity

In order to determine whether there were differences in phylogenetic diversity of indigenous parasitoids, I used the same procedure and analyses as in Appendix 3.2. Given that some of the parasitoids were only identified to morpho-species level, I only conducted these analyses for specimens formally identified to species by Linnean classification, and

specimens belonging to a genus for which no alien species have been registered in New Zealand (*Aleiodes, Aucklandella, Campoletis, Campoplex, Carria, Choeras, Genotrichia, Genus nov.Hearthhead, Ophion, Pales, Phytodietus, Uclesiella* and *Zealachertus*). Morphospecies that belonged to genera containing both indigenous and alien species were excluded from the analyses, because of their uncertain origin.

I did not find differences in phylogenetic diversity (PSV, PSR or PSE) of indigenous parasitoids across the habitat edge gradient (Table S3.2, Fig. S3.2).

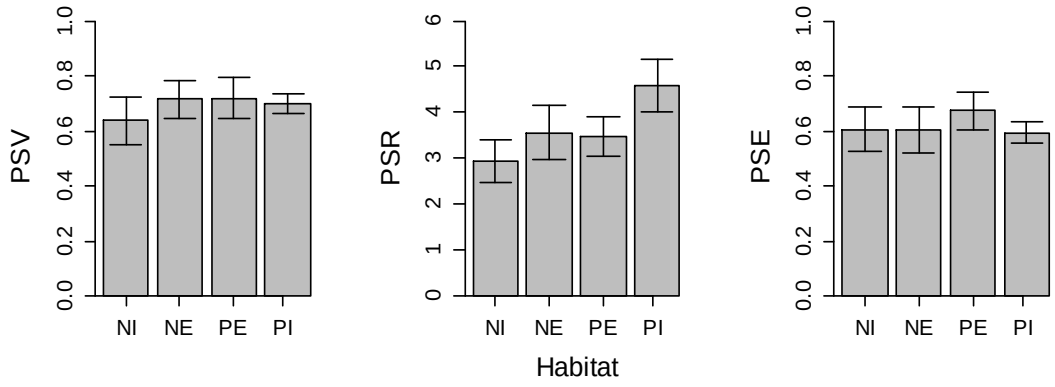

Figure S3.2: Mean (± SE) of phylogenetic species variability (PSV), phylogenetic species richness (PSR) and phylogenetic species evenness (PSE) of indigenous parasitoid species across a habitat edge gradient. NI = native forest interior habitat, NE = native forest edge, PE = plantation forest edge, PI = plantation interior habitat.

Table S3.2: Results from GLMMs (with Gaussian distribution) showing differences in parasitoid phylogenetic diversity across forest types (native vs. plantation) and location (edge vs. interior). Results are from the best-fitting models (with lowest AIC), after model selection. P-values were estimated using a Markov Chain Monte Carlo procedure. Herbivore abundance was entered as a covariate in all the models. PSV = phylogenetic species variability, PSR = phylogenetic species richness, PSE = phylogenetic species evenness. Bold values indicate significant results ($\alpha = 0.05$). Forest P = Plantation forest; Location I = interior location.

Phylogenetic diversity metric	Fixed effects	Estimate ± SE	t-value	P_{MCMC}
Parasitoid PSV	Intercept	0.755 ± 0.095	7.939	**<0.001**
	Herbivore abundance	< -0.001 ± < -0.001	-0.740	0.535
	Forest P	0.051 ± 0.071	0.720	0.504
	Location I	-0.041 ± 0.063	-0.643	0.563
Parasitoid PSR	Intercept	1.818 ± 0.664	2.737	**0.018**
	Herbivore abundance	0.009 ± 0.003	2.646	0.077
	Forest P	0.399 ± 0.618	0.646	0.383
	Location I	0.114 ± 0.334	0.342	0.745
Parasitoid PSE	Intercept	0.741 ± 0.087	8.476	**<0.001**
	Herbivore abundance	-0.001 ± 0.0005	-1.823	0.099
	Forest P	0.068 ± 0.066	1.034	0.355

References

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Appendix 4

Appendix 4.1: Supplementary figures

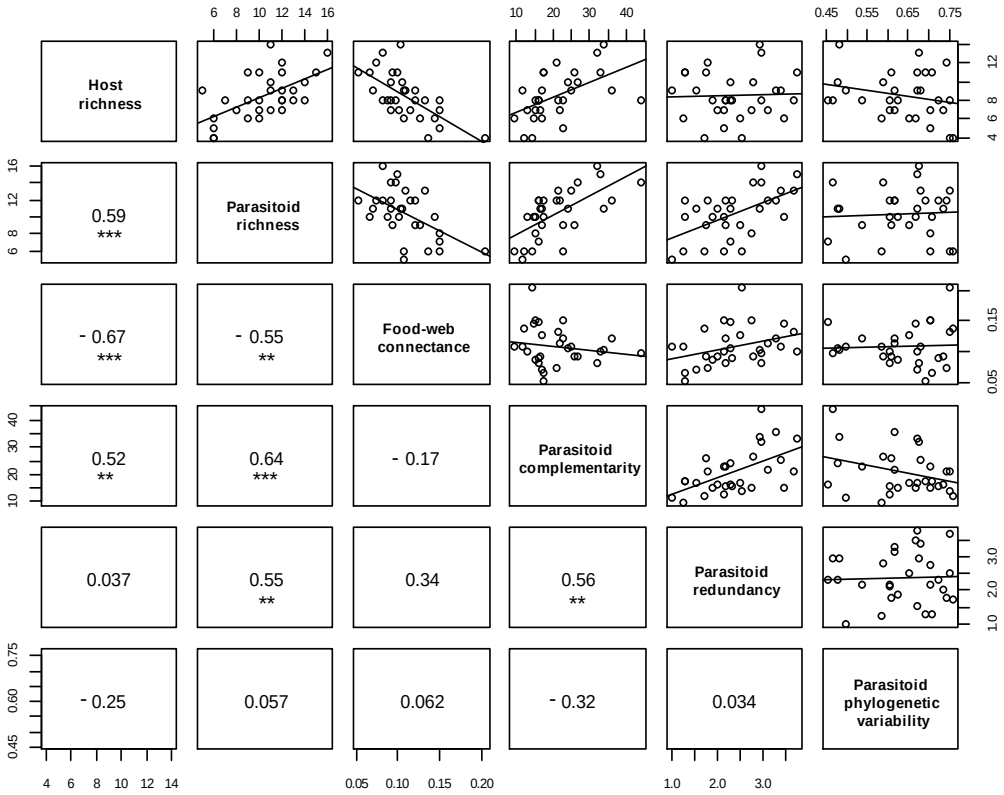

Figure S4.1: Scatterplots and associated Pearson correlation coefficients for the pairwise relationships among covariates (host species richness, parasitoid species richness and food-web connectance) and predictor variables (parasitoid complementarity, parasitoid redundancy and parasitoid phylogenetic variability). * = P < 0.05, ** = P < 0.01, *** = P < 0.001.

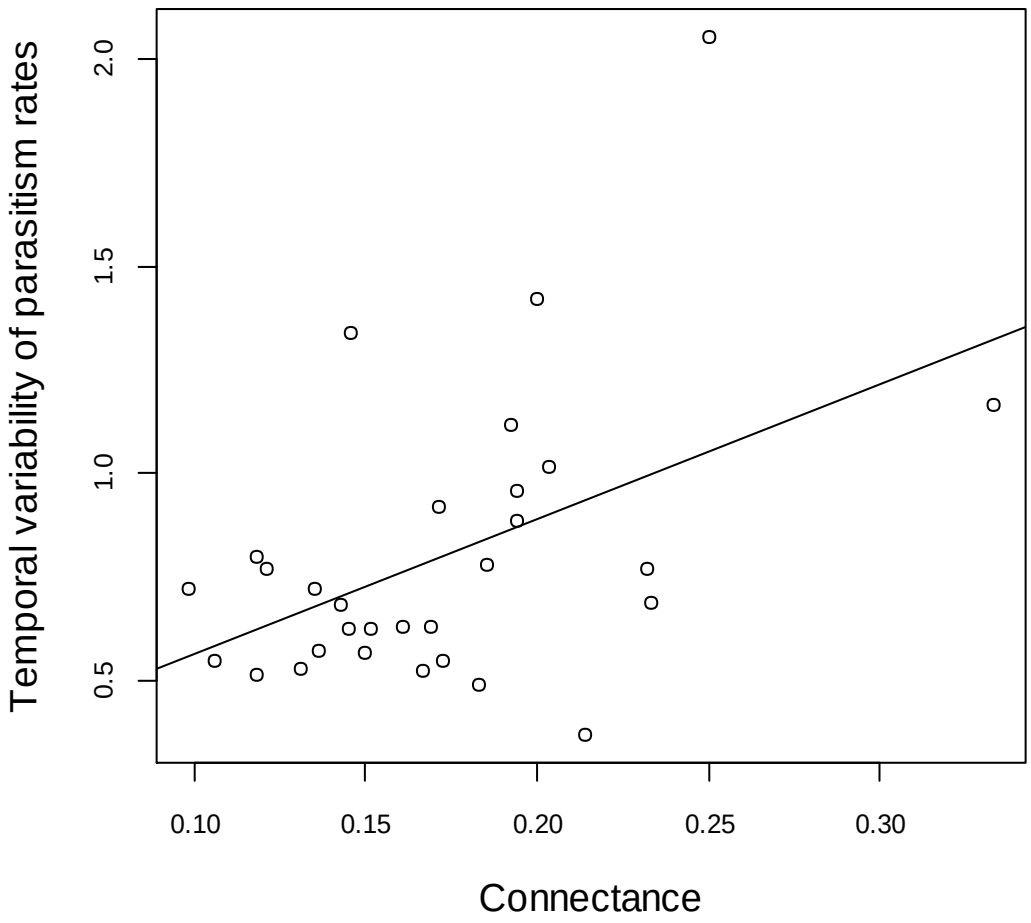

Figure S4.2: Relationship between temporal variability of parasitism rates (measured as the coefficient of variation of parasitism rates trough time) and connectance (the weighted number of realized links divided by the number of possible parasitoid-host combinations). The solid line represents a significant relationship between variables ($t = 3.453$, $P_{MCMC} = 0.009$).

Appendix 4.2: Supplementary tables

Table S4.1: Best-fitting model results for generalized linear mixed-effects models testing the effect of community and food-web metrics on A) cumulative parasitism rates (with binomial error, Z-test); B) temporal variability of parasitism rates, measured as the coefficient of variation of parasitism rates through time (with Gaussian error, t-value, p-values estimated by Markov Chain Monte Carlo procedure); C) spatial variability of parasitism rates, measured as the coefficient of variation of parasitism rates through space. Host and parasitoid species richness, and connectance (the weighted number of realized links) were entered as covariates, and their removal was not allowed during model selection. Bold values indicate significant results ($\alpha = 0.05$).

Response variable	**Fixed effects**	**Estimate ± SE**	**Z/t-value**	**P-value (P_{MCMC})**
A) Parasitism rates	Intercept	-2.258 ± 0.514	-4.394	**<0.001**
	Host richness	-0.019 ± 0.029	-0.664	0.506
	Parasitoid richness	0.012 ± 0.025	0.501	0.616
	Connectance	-1.506 ± 2.492	-0.604	0.546
	Parasitoid functional complementarity	0.016 ± 0.007	2.238	**0.025**
B) Temporal variability of parasitism rates	Intercept	-0.082 ± 0.651	-0.126	0.631
	Host richness	-0.011 ± 0.030	-0.367	0.806
	Parasitoid richness	-0.040 ± 0.024	-1.673	0.597
	Connectance	1.611 ± 1.755	0.918	0.352
C) Spatial variability of parasitism rates	Intercept	-0.239 ± 0.487	-0.491	0.657
	Host richness	0.007 ± 0.008	0.843	0.461
	Parasitoid richness	0.007 ± 0.008	0.981	0.399
	Connectance	3.566 ± 2.767	1.289	0.288
	Parasitoid redundancy	-0.065 ± 0.029	-2.271	0.108

Appendix 4.3: Description of quantitative food-web metrics

Redundancy: A measurement of parasitoid redundancy was estimated by the diversity of parasitoids attacking each host, also known as food-web vulnerability. I used a quantitative version (V_q) (Bersier *et al.* 2002), which is known to be less sensitive to

sampling effects than the presence/absence version (Banasek-Richter *et al.* 2004), and is calculated as:

$$V_q = \sum_{k=1}^{s} \frac{b_{k\bullet}}{b_{\bullet\bullet}} n_{P,k}$$

where $b_{k\bullet}$ represents the total number of individuals (parasitoids) attacking host species *k*, $n_{P,k}$ the reciprocal of diversity of parasitoids and $b_{\bullet\bullet}$ number of parasitoids attacking all host species.

Connectance: In order to determine the proportion of realized interactions (links) weighted by their frequency of occurrence (quantitative connectance, C_q), I calculated the quantitative version of linkage density for each food web (LD_q) and then divided it by the number of host and parasitoid species (S) (Bersier *et al.* 2002). Linkage density was calculated as:

$$LD_q = \frac{1}{2}\left(\sum_{k=1}^{s} \frac{b_{x\bullet}}{b_{\bullet\bullet}} n_{P,k} + \sum_{k=1}^{s} \frac{b_{\bullet k}}{b_{\bullet\bullet}} n_{N,k} \right)$$

where $b_{\bullet k}$ represents the total number of individuals (hosts) attacked by parasitoid species *k* *and* $n_{N,k}$ the reciprocal of diversity of hosts.

Appendix 4.4: Leverage calculation.

I calculated the leverage of each point (h_i) according to Crawley (Crawley 2007):

$$h_i = \frac{1}{n} + \frac{(x_i - \bar{x})^2}{\sum (x_j - \bar{x})^2}$$

where n represents the number of data points, x_i the value of point i, $\bar{x}$ the mean and x_j the values of the other points of the variable.

A point is highly influential if the measure of leverage of a point (h_i) is higher than two times the number of parameters (p) divided by the number of samples (n):

$$h_i > \frac{2p}{n}$$

Of the 32 food webs, two presented potentially highly-influential values: one for parasitoid functional redundancy (Fig. S4.3.A), and the other for parasitoid functional complementarity (Fig. S4.3.B). Given the potential for these values to affect model estimates, I removed these two webs from all the analyses.

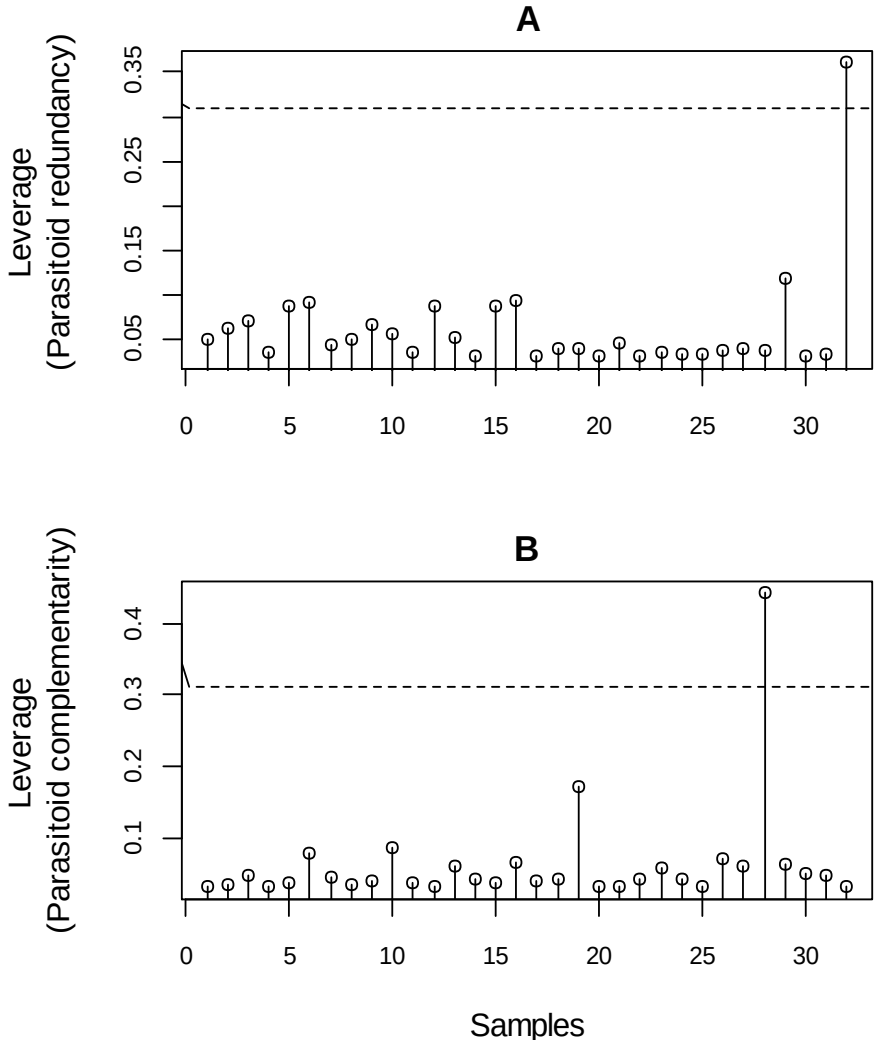

Figure S4.3: Leverage values of A) parasitoid redundancy (food-web vulnerability) and B) parasitoid functional complementarity for each of the 32 host-parasitoid webs sampled. The dashed line represents the lower limit of highly influential points, i.e. points above the line are considered to be highly-influential (with leverage values > $2p/n$). Webs number 32 and 28 had high leverage for redundancy and complementarity respectively.

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